DURHAM, N. C.
JUL 27 1938

VOLUME 24 JULY, 1938 NUMBER 7

PROCEEDINGS

OF THE

NATIONAL ACADEMY OF SCIENCES

OF THE

UNITED STATES OF AMERICA

EXECUTIVE COMMITTEE

EDWIN BIDWELL WILSON, *Managing Editor*

RAYMOND PEARL LUDVIG HEKTOEN

PUBLISHED MONTHLY

Publication Office: Mack Printing Company, Easton, Pa.

Editorial Office: Harvard School of Public Health, Boston 17

Home Office of the Academy: Washington, D. C.

...tered as second-class matter June 21, 1920, at the post-office at Easton, Pennsylvania, under the act of August 24, 1912. ...ccepted for mailing at a special rate of postage, provided for in section 1103, act of October 3, 1917. Authorized June 18, 1920.

Price per annum, $5.00

OFFICERS OF THE ACADEMY

PRESIDENT ..... F. R. LILLIE
VICE PRESIDENT ..... A. L. DAY
FOREIGN SECRETARY ..... L. J. HENDERSON
HOME SECRETARY ..... FRED. E. WRIGHT
TREASURER ..... ARTHUR KEITH

EDITORIAL BOARD

The HOME SECRETARY and the FOREIGN SECRETARY of the ACADEMY
The CHAIRMAN OF THE NATIONAL RESEARCH COUNCIL

V. BUSH	L. J. HENDERSON	W. R. MILES
R. E. COKER	W. S. HUNTER	R. A. MILLIKAN
A. L. DAY	F. B. JEWETT	H. R. MOODY
L. P. EISENHART	A. B. LAMB	W. J. V. OSTERHOUT
R. G. HARRISON	E. R. LONG	F. K. RICHTMYER
L. HEKTOEN	C. R. LONGWELL	F. H. SEARES

INFORMATION TO SUBSCRIBERS

SUBSCRIPTIONS TO THE PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES at the rate of $5.00 per annum should be made payable to the National Academy of Sciences, and sent to the Home Secretary, National Academy of Sciences, Constitution Ave. & 21st Street, Washington, D. C. Single numbers, $0.50.

PAST publications of the NATIONAL ACADEMY OF SCIENCES from 1863 to 1926 and of the NATIONAL RESEARCH COUNCIL from 1916 to 1925 are listed in the Index to the First Ten Volumes of these PROCEEDINGS. This Index appeared as Part 2 of Volume 13, No. 1, January, 1927, and is for sale separately at the price of $1.50. Orders should be sent to the Home Secretary, National Academy of Sciences, Constitution Ave. & 21st Street, Washington, D. C.

PAST volumes of the PROCEEDINGS may be obtained at five dollars per volume unless the sale of the volume would break a complete set of Volumes I to X. Single numbers may be obtained for fifty cents except where the sale of such numbers would break up a complete volume. Only two hundred complete sets of the PROCEEDINGS are available for sale—Volume I to X, price $75.00 (including Index, see *supra*). Orders should be sent to the Home Secretary, National Academy of Sciences, Constitution Ave. & 21st Street, Washington, D. C.

The following publications are issued by the NATIONAL RESEARCH COUNCIL. Orders and inquiries should be addressed: Publication Office, National Research Council, Constitution Ave. & 21st Street, Washington, D. C.

(A) THE BULLETIN OF THE NATIONAL RESEARCH COUNCIL published at irregular intervals. Individual numbers priced variously. A discount of 20% from the list price will be given to all who subscribe for the series as issued, direct from the Publication Office.

(B) THE REPRINT AND CIRCULAR SERIES OF THE NATIONAL RESEARCH COUNCIL, individual numbers variously priced. A discount of 20% from the list price will be given to all who subscribe for the series as issued, direct from the Publication Office.

PROCEEDINGS
OF THE
NATIONAL ACADEMY OF SCIENCES
Volume 24 July 15, 1938 Number 7
Copyright 1938 by The National Academy of Sciences

THE DISTRIBUTION OF GENE FREQUENCIES UNDER IRREVERSIBLE MUTATION

By Sewall Wright

Department of Zoölogy, The University of Chicago

Communicated June 13, 1938

Under reversible mutation, the frequency (q) of a gene, subject to systematic evolutionary pressure (Δq) and to the accidents of sampling in a limited population (N diploid individuals), varies according to a certain distribution ($\varphi(q)$) discussed in previous papers.[1,2,3] If mutation is irreversible, the distribution curve for such genes should attain constancy of form, but all class frequencies should fall off at a uniform rate (K) as genes drift irreversibly into fixation. The purpose of the present paper is to broaden somewhat the treatment in this latter case.

As previously shown[2] the rate of fixation is approximately half the frequency, $f(1 - 1/2N)$, in the subterminal class. Thus with

$$\int_0^1 \varphi(q)dq = 1$$

$$K = 1/2\, f(1 - 1/2N) = \frac{\varphi(1 - 1/2N)}{4N} \quad \text{approximately.} \qquad (1)$$

The changes in the mean ($\bar{q} = \int_0^1 q\varphi(q)dq$) and the variance ($\sigma_q^2 = \int_0^1 (q - \bar{q})^2\varphi(q)dq$) of gene frequencies, due to fixation in one generation, may be expressed as follows in terms of the systematic evolutionary pressure, Δq, and the variation due to sampling, $\sigma_{\Delta q}^2$

$$\int_0^1 \Delta q\varphi(q)dq = K(1 - \bar{q}). \qquad (2)$$

$$\int_0^1 (q + \Delta q - \bar{q})^2\varphi(q)dq + \int_0^1 \sigma_{\Delta q}^2\varphi(q)dq = (1 - K)\sigma_q^2 + K(1 - \bar{q})^2. \qquad (3)$$

The latter can be reduced to following, ignoring a negligible term in $(\Delta q)^2$

$$2\int_0^1 (q - \bar{q})\,\Delta q\varphi(q)dq + \int_0^1 \sigma^2_{\Delta q}\varphi(q)dq = K[(1 - \bar{q})^2 - \sigma^2_q]. \quad (4)$$

If the conditions are such that under equilibrium, with reverse mutation at an indefinitely low rate, there is no important accumulation of genes in the class $q = 1$, complete irreversibility of mutation should make no appreciable difference in the form of distribution. The demonstration of the formula for this case ($K = 0$) can be put in a very simple form.

$$\text{Let} \quad \int \Delta q\varphi(q)dq = \chi(q). \quad (5)$$

Equations (2) and (4) can be written as follows, putting $K = 0$,

$$\chi(1) - \chi(0) = 0. \quad (6)$$

$$\int_0^1 \chi(q)dq - [\bar{q}\chi(0) + (1 - \bar{q})\chi(1)] - \frac{1}{2}\int_0^1 \sigma^2_{\Delta q}\varphi(q)dq = 0. \quad (7)$$

Equation (7) is obviously satisfied by the following

$$\chi(q) - [\bar{q}\chi(0) + (1 - \bar{q})\chi(1)] - \frac{1}{2}\sigma^2_{\Delta q}\varphi(q) = 0. \quad (8)$$

This means little, until it is shown that (8) also satisfies (6).

As there can be no sampling variance in homallelic populations, $\sigma^2_{\Delta q} = 0$ if $q = 0$ or $q = 1$. Equation (8) reduces to (6) if $q = 0$ or $q = 1$ and both $\varphi(0)$ and $\varphi(1)$ are finite. Equation (8), therefore, satisfies the condition of constancy of the mean as well as that of constancy of the variance.

$$\varphi(q) = \frac{2[\chi(q) - \chi(1)]}{\sigma^2_{\Delta q}}. \quad (9)$$

$[\chi(q) - \chi(1)]$ can be evaluated as follows, using (5) and (9),

$$d \log [\chi(q) - \chi(1)] = \frac{d\chi(q)}{\chi(q) - \chi(1)} = \frac{2\,\Delta q\varphi(q)dq}{\sigma^2_{\Delta q}\varphi(q)}, \quad (10)$$

$$\chi(q) - \chi(1) = \frac{C}{2}\,e^{2\int \frac{\Delta q dq}{\sigma^2_{\Delta q}}}, \quad (11)$$

$$\varphi(q) = \frac{Ce^{2\int (\Delta q/\sigma^2_{\Delta q})dq}}{\sigma^2_{\Delta q}}. \quad (12)$$

This is the desired expression for the distribution in terms of Δq and $\sigma^2_{\Delta q}$.

Putting $\sigma^2_{\Delta q} = \frac{q(1 - q)}{2N}$, its value in a population of N diploid indi-

viduals, it is the same as the formula given previously[3] (except for the value of the coefficient C).

If K is not zero, this method does not appear to lead to a usable general expression which satisfies (1), (2) and (4). An expression for the rate of decay can, however, be obtained from (2). Let v be the rate of mutation, and let $\overline{W}$ be the mean selective value of genotypes. As shown previously[3]

$$\Delta q = v(1 - q) + q(1 - q)\frac{d \log \overline{W}}{2dq}. \tag{13}$$

From (2) $$K = v + \frac{1}{2(1 - \bar{q})}\int_0^1 q(1 - q)\varphi(q)d \log \overline{W}. \tag{14}$$

If there is no selection ($\overline{W} = 1$)

$$K = v. \tag{15}$$

The distribution (16) for this case was obtained in a previous paper[2] by substitution of $\Delta q = v(1 - q)$ in what is equation (18) of the present paper. It can easily be verified that (16) also satisfies (1), (2) and (4).

$$\varphi(q) = 4Nvq^{4Nv-1}. \tag{16}$$

The most important cases are probably those in which the size of population is so small that recurrent mutation has no effect on the form of distribution (v much less than $1/4N$). The selection pressure for any degree of dominance can be written sufficiently accurately

$$\Delta q = (s + tq)q(1 - q). \tag{17}$$

The condition that the frequency of any class of gene frequencies, q_c, be reconstructed after each generation, except for a uniform decay at rate K can be represented as follows,[2] using $p = 1 - q$ for brevity.

$$(1 - K)\varphi(q_c) = A\int_0^1 (q + \Delta q)^{2Nq_c}(p - \Delta q)^{2Np_c}\varphi(q)dq$$

where $$A = \frac{\Gamma(2N)}{p_c q_c \Gamma(2Np_c)\Gamma(2Nq_c)}. \tag{18}$$

If v is so small that practically all genes are fixed in the class $f(0)$, K may be ignored in determining the form of the distribution for unfixed genes. Substituting the value of Δq from (17)

$$\varphi(q_c) = A\int_0^1 q^{2Nq_c}p^{2Np_c}[1 + p(s + tq)]^{2Nq_c}[1 - q(s + tq)]^{2Np_c}\varphi(q)dq. \tag{19}$$

The following approximations may be used

$$[1 + p(s + tq)]^{2Nq_c} = e^{2Nq_cp(s+tq)}\ [1 - Nq_cp^2(s + tq)^2]. \tag{20}$$

$$[1 - q(s + tq)]^{2Np_c} = e^{-2Np_cq(s+tq)}[1 - Np_cq^2(s + tq)^2]. \quad (21)$$

The product of expressions (20) and (21) is approximately

$$e^{2Ns(q_c-q)+Nt(q^2_c-q^2)-Nt(q_c-q)^2}\left\{1 - N(s + tq)^2[p_cq_c + (q_c - q)^2]\right\}. \quad (22)$$

Since the random deviations of q have the variance, $\sigma^2_{\Delta q} = \frac{pq}{2N}$, $(q_c - q)^2$ is of the order $1/2N$. The term $N(s + tq)^2(q_c - q)^2$ is thus negligibly small compared with $N(s + tq)^2p_cq_c$ which itself is as small a term as it is necessary to consider. The former may thus be ignored. The constant and variable gene frequencies are separable in the exponential term in (22) except in the term $e^{-Nt(q_c-q)^2}$. The exponent in this case is smaller than $-t$ and the term can be written $[1 - Nt(q_c - q)^2]$ with sufficient accuracy. Equation (19) can now be written as follows:

$$\varphi(q_c) = Ae^{2Nsq_0 + Ntq^2_c}\int_0^1 q^{2Nq_c}p^{2Np_c}e^{-2Nsq-Ntq^2}\,[1 - N(s + tq)^2p_cq_c - Nt(q_c - q)^2]\varphi(q)dq. \quad (23)$$

Let $$\varphi(q) = \frac{e^{2Nsq + Ntq^2}}{q\ (1-q)}\,(C_0 + C_1q + C_2q^2 \ldots). \quad (24)$$

This entirely eliminates the exponential terms, leaving (23) in a form which can be solved, using the following sufficiently accurate formula in which terms of the order $\frac{1}{N^2}$ are ignored.

$$\frac{\Gamma(2N)}{\Gamma(2Np_c)\Gamma(2Nq_c)}\int_0^1 q^{2Nq_c-1+x}\,p^{2Np_c-1}\,dq = q_c^x\left[1 - \frac{x(x-1)}{4N}\right] + q_c^{x-1}\left[\frac{x(x-1)}{4N}\right]. \quad (25)$$

The resulting coefficients of the powers of q_c on the right side may be equated to those on the left side leading to the following general expression (in which $C_{-1} = C_{-2} = C_{-3} = 0$).

$$C_m = \frac{m(m+1)}{4N}\,C_{m+1} + C_m - \frac{C_{m-1}}{2}\,(2Ns^2 + t) - C_{m-2}\,(2Nst) - C_{m-3}\,Nt^2. \quad (26)$$

The higher coefficients can all be expressed in terms of C_0 and C_1 and substituted in (24). By letting $C_1 = 2NsC_0 + D$ the terms for which C_0 is the coefficient can be condensed into exponential form. It will be convenient to substitute C for C_0.

$$\varphi(q) = \frac{e^{2Nsq + Ntq^2}}{q(1-q)}\left[Ce^{2Nsq + Ntq^2} + Dq\psi(q)\right], \tag{27}$$

where

$$\psi(q) = 1 + \frac{(2Nsq)^2}{|\underline{3}} + \frac{(2Nsq)^4}{|\underline{5}} + \frac{(2Nsq)^6}{|\underline{7}} \cdots \tag{28}$$

$$+ (2Ntq^2)\left(\frac{1}{|\underline{3}} + \frac{(2Nsq)}{|\underline{3}} + \frac{2(2Nsq)^2}{|\underline{5}} + \frac{2(2Nsq)^3}{|\underline{5}} + \frac{3(2Nsq)^4}{|\underline{7}} \cdots\right)$$

$$+ (2Ntq^2)^2\left(\frac{7}{|\underline{5}} + \frac{2(2Nsq)}{|\underline{5}} + \frac{69(2Nsq)^2}{|\underline{7}} \cdots\right)$$

$$+ (2Ntq^2)^3\left(\frac{27}{|\underline{7}} \cdots\right) + \cdots$$

If $D = 0$

$$\varphi(q) = \frac{Ce^{4Nsq + 2Ntq^2}}{q(1-q)}. \tag{29}$$

This is the case of equilibrium under reversible mutation or irreversible mutation opposed by sufficiently strong selection as can be seen by substituting $\Delta q = (s + tq)q(1-q)$, $\sigma^2_{\Delta q} = \frac{q(1-q)}{2N}$ in (12). They agree except in the coefficient.

The case of irreversible mutation with fixation occurring at a low rate, can be found from (1) and (2), assuming that nearly all genes are in one of the homallelic classes. It should be noted that the formula for $\varphi(q)$ only applies where K is of lower order than $1/2N$, $2Ns^2 + t$ in (26). Mutations to the class $q = 1/2N$ contribute the amount $2Nvf(0) = \frac{1}{2}f(1/2N)$ and these contribute to the change of mean by the amount $f(1/2N)/4N$. The mean, however, must be so low that the term $K(1-\bar{q})$ may be written K sufficiently accurately. The following relations are all approximate:

$$\int_0^1 \Delta q\varphi(q)dq + \frac{f(1/2N)}{4N} = K = \frac{f(1-1/2N)}{2}. \tag{30}$$

$$f(1/2N) = C\left[1 + \frac{1}{2N} + 2s\right] + \frac{D}{2N}. \tag{31}$$

$$f(1-1/2N) =$$
$$C[e^{4NS + 2Nt}(1 + 1/2N - 2s - 2t)] +$$
$$D[e^{2Ns + Nt}(1 - s - t)\psi(1 - 1/2N)]. \tag{32}$$

$$\int_0^1 \Delta q\varphi(q)dq = C\left[\frac{e^{4Ns+2Nt}}{4N} - \frac{1}{4N}\right] + \frac{Ds}{2} + \frac{Dt}{3}. \qquad (33)$$

Substituting (31), (32), (33) in (30) and substituting $\psi(1)$ for $\psi(1 - 1/2N)$ (leading terms in difference, $t/3$, $\frac{2Ns^2}{3}$)

$$D = -\frac{Ce^{2Ns+Nt}}{\psi(1)}. \qquad (34)$$

With practically all genes in the class $q = 0, f(0) = 1 = \frac{f(1/2N)}{4Nv} = \frac{C}{4Nv}$. Thus $C = 4Nv$ approximately.

$$\varphi(q) = \frac{4Nve^{4Nsq+2Ntq^2}}{q(1-q)}\left[1 - \frac{e^{2Ns(1-q)+Nt(1-q^2)}q\psi(q)}{\psi(1)}\right]. \qquad (35)$$

For sufficiently small values of Ns and Nt we may take $\psi(q) = 1 + 1/3Ntq^2$ and represent the exponentials by the first two terms of their expansions. The following shows how the hyperbolic distribution $4Nv/q$ is modified by weak selection (s positive for favorable mutation, negative for unfavorable mutation).

$$\varphi(q) = \frac{4Nv}{q}[1 + 2Nsq + 2/3Ntq(2q - 1)]. \qquad (36)$$

The rate of fixation (K) of genes can be found from the left member of (30) (in which inaccuracies in the evaluation of D have less effect than in the right member).

$$K = v\left[e^{4Ns+2Nt} - \frac{(2Ns + 4/3Nt)e^{2Ns+Nt}}{\psi(1)}\right]. \qquad (37)$$

This reduces to $v(1 + 2Ns + 2/3Nt)$ for such small values of Ns and Nt as implied in (36). It is to be noted that irreversible mutation should ultimately lead to fixation of the mutant even when opposed by selection (s negative) but the rate is exceedingly slow unless Ns and Nt are small.

In the special case of genic selection ($t = 0$)

$$\psi(q) = \frac{e^{2Nsq} - e^{-2Nsq}}{4Nsq}. \qquad (38)$$

$$\varphi(q) = \frac{4Nv}{(1 - e^{-4Ns})}\frac{[1 - e^{-4Ns(1-q)}]}{q(1-q)}. \qquad (39)$$

An essentially similar derivation of this formula has been given previously by the author[2] and a different one by Fisher.[4] In this case $K = \frac{4Nvs}{1 - e^{-4Ns}}$ approaching $v(1 + 2Ns)$ as $4Ns$ decreases.

The question of the chance of fixation of an individual mutation must be distinguished from the rate of fixation (K) under recurrent mutation. The chance of fixation is given by the ratio $f(1 - 1/2N)/f(1/2N) = K/2Nv$. In the case of no dominance, this gives $2s/(1 - e^{-4Ns})$ or approximately $2s$ for favorable mutations occurring in a large population, in agreement with Fisher.[4] For indifferent factors it is $1/2N$ Unfavorable mutations have a chance of fixation $2s/(e^{4Ns} - 1)$ but this is small unless $4Ns$ is small.

The results presented here bear on the possibility of a course of evolutionary change determined by mutation pressure, a process which at first sight seems the most obvious implication of modern genetics. The possibility does indeed exist but requires either an almost complete indifference of the mutation with respect to adaptive value or else a very small effective size of population over a long period of time. The most important case in which mutation pressure seems likely to be a major factor is that of extreme degeneration or elimination of organs that have ceased to be useful.[5,6] The degeneration of the eyes and loss of pigment of cave forms is an example of a case in which the conditions make it especially probable that mutation pressure is a real factor. In all of these cases, however, the likelihood that various direct and indirect effects of selection may also play a rôle should not be ignored.[5]

It should be noted that while the average rate of fixation of irreversible mutations is low, the large element of chance with respect to *which* mutations become fixed in each particular case makes this a greater factor in the diversification of small isolated populations than is at first apparent. Indeed there may be much diversification of gene frequencies among such populations under conditions in which there is no appreciable systematic tendency toward fixation of the sort investigated here.

[1] Wright, S., *Amer. Nat.*, **63**, 556–561 (1929).
[2] Wright, S., *Genetics*, **16**, 97–159 (1931).
[3] Wright, S., *Proc. Nat. Acad. Sci.*, **23**, 307–320 (1937).
[4] Fisher, R. A., *Proc. Roy. Soc. Edinburgh*, **50**, 205–220 (1930)
[5] Wright, S., *Amer. Nat.*, **63**, 274–279 (1929).
[6] Haldane, J. B. S., *Ibid.*, **67**, 5–19 (1933).

AUXIN IN ISOLATED ROOTS GROWING IN VITRO[13]

BY J. VAN OVERBEEK AND JAMES BONNER

WILLIAM G. KERCKHOFF LABORATORIES OF THE BIOLOGICAL SCIENCES, CALIFORNIA INSTITUTE OF TECHNOLOGY

Communicated June 15, 1937

Up to the year 1933 opinion was divided as to whether or not auxin is present in the root. In this year Boysen-Jensen[1] conclusively demonstrated that auxin is present in the normal root. With respect to the isolated root, however, Fiedler[2] has reported that auxin, although initially present, disappears completely and in general within 24 hours, when the root is cultivated *in vitro*. Nagao[3] on the other hand, has shown that auxin may be recovered from isolated roots after 6 days' cultivation *in vitro*. The object of the present work has been primarily to establish, with the aid of improved techniques, whether or not auxin is actually present in isolated roots cultivated *in vitro*. A second but related problem of whether or not auxin is *produced* by such roots will be dealt with in a later communication although experiments of a preliminary nature indicate that it is not produced but is merely carried along in the tip of the isolated root.

Methods.—Pea roots were cultivated *in vitro* under the conditions which have been described elsewhere.[4] Tips ca. 4 mm. long were removed from the roots of germinating pea seeds[5] and cultured under strictly sterile conditions in 10 cm. Petri dishes in a basic nutrient solution containing sucrose, inorganic salts, vitamin B_1 (0.1 mg. per liter) and varying amounts of certain amino acids. After the roots had grown for one week and were ca. 70 mm. long, they were subcultured by removal of a 10 mm. tip to fresh medium. If the roots were to be further subcultured this procedure was repeated at weekly intervals. Since lateral roots are formed only after approximately 10 days' culture *in vitro* under these conditions, these experiments are uncomplicated by the presence of more than one growing point per root.

The technique of the auxin extraction and determination has been described in detail elsewhere.[6] The material to be extracted was placed in highly purified ether, in the cold room (ca. 2°C.) for 15 to 30 hours. The material was neither ground nor acidified[7] since either of these procedures may result in a partial destruction of auxin. The ether extract was then evaporated to dryness and taken up in a known amount of hot agar (1.5%). This agar was in turn analyzed for auxin by means of the *Avena* test. For each determination 24 test plants were used. In order that the auxin content of the roots might be expressed in "indole-acetic acid equivalents," comparable controls with this substance were also run. In general

two concentrations, one of 20 gamma and one of 7 gamma per liter were used for these controls. Each control was also run with 24 test plants. A blank with plain agar blocks was also included in each test. In an earlier paper[8] it has been pointed out that the *Avena* curvature-concentration curve often does not pass through the origin, but that it intersects the abscissa. This means that the curvature is not directly proportional to the concentration. There is a certain "threshold concentration" before a curvature is obtained. This threshold concentration, which is in general about 5 gamma per liter, was determined for most of the tests and was applied to the subsequent calculations. It was, however, found that if this threshold concentration is taken into account, the relationship between auxin concentration and *Avena* curvature can be expressed by a straight line,[9] at least under the conditions of these experiments.

The auxin content of the roots was calculated according to the following formula:

$$\text{auxin concentration} = \frac{(C \times I_1^\circ + O) \times V_{agar}}{W}$$ gamma indole acetic acid equivalents per kg. fresh weight

C = the average curvature obtained in the *Avena* test (extracted material)

I_1° = indole acetic acid concentration giving an increase of 1° in the *Avena* test, in gamma per liter

O = threshold concentration, gamma indole acetic acid per liter

V_{agar} = volume of agar in which the dry extract was taken up, cc.

W = fresh weight of material under investigation, gms.

Auxin Concentration in Roots.—Table 1 shows that under the conditions of our experiments auxin is present in isolated pea roots cultivated *in vitro* even after three weeks, and consequently, after 2 subcultures. There can then be no doubt but that auxin may be present in relatively large amounts, even in the cultured root. Fiedler,[2] as mentioned above, failed to find auxin in isolated roots (*Zea*, *Pisum*, *Vicia*) after more than 48 hours' growth *in vitro*. That Fiedler failed to extract auxin from *Zea* roots of any age, is undoubtedly due to the extraction technique which he employed. It has been shown elsewhere[6] that auxin cannot in general be obtained from *Zea* if acid is employed in the extraction (acid was used by Fiedler). It is shown in table 2 that with the present extraction technique, auxin can be obtained from the roots of sterile, germinating *Zea* seeds. The amount present in these roots is smaller than that present in *Pisum* roots of the same length (table 2). It has been shown earlier[6] that the shoots of *Zea* seedlings, also, contain less auxin than do the shoots of corresponding *Pisum* seedlings. The failure of Fiedler to extract auxin

from isolated pea roots cannot, however, be satisfactorily explained, although this also may have been due to the different techniques employed.

Nature of the Hormone Present.—It was of importance to ascertain whether the auxin of these roots was auxin-a, auxin-b or hetero-auxin (indole acetic acid). This may conveniently be determined by the differential acid-alkali destruction test of Kögl, Haagen-Smit and Erxleben.[10]

TABLE 1

AUXIN CONCENTRATIONS FOUND IN ISOLATED ROOTS GROWING *in vitro*, GAMMA "INDOLE ACETIC ACID EQUIVALENTS" PER KG. FRESH WEIGHT. THE CULTURES WERE ANALYZED ONE WEEK AFTER THEY WERE STARTED. CULTURES OF "ALASKA" ROOTS ARE INDICATED BY A, THOSE OF "PERFECTION" BY P. I, II, III, ETC., ADDED TO A OR P INDICATE RESPECTIVELY THE FIRST CULTURE, SECOND CULTURE (FIRST SUBCULTURE), THIRD CULTURE, ETC. THUS THE P III CULTURE AT THE TIME IT WAS ANALYZED HAD BEEN CONTINUED THREE WEEKS SINCE THE INITIAL ROOT TIP WAS CUT FROM THE EMBRYO

EXPT. NUMBER	CULTURE	γ/KG.	REMARKS
80315	A I	1.69	
80413	A I	2.24	no tip
80418	A II	5.88	
...	...	7.48	
80429	A II	6.40	
80517	roots 4 mm. long from embryo, P 0	22.3	
80315	P I	2.26	
80315	P II	2.28	
80331	P II	2.45	
80418	P III	4.12	

TABLE 2

AUXIN CONCENTRATION AND CONTENT OF 1-CM.-LONG ROOTS OF GERMINATING *Zea*, AND *Pisum* SEEDS. GAMMA "INDOLE ACETIC ACID EQUIVALENTS"

EXPT. NUMBER	PLANTS	C	$(C \times I_1^{\circ} + O)$	V_{agar}	W	γ/KG.	γ/PER ROOT
80603	*Zea*	3.0	9.4	0.5	2.60	**1.64**	**20.6×10^{-6}**
80523	Alaska	10.6	23.6	10.0	6.60	**36.0**	**300.0×10^{-6}**
80523	Perfection	7.8	18.0	7.5	4.00	**35.3**	**268.0×10^{-6}**
		3.5	9.8	15.0	4.00		

This test is based on the facts (*a*) that indole acetic acid is heat stable to alkali but is destroyed by acid, (*b*) that auxin-a is stable to acid but is destroyed by alkali and (*c*) that auxin-b is unstable to both acid and alkali. Three separate tests of this nature showed that the auxin extracted from pea roots was completely destroyed by alkali, unaffected by acid and must hence have been auxin-a. It might be mentioned in this connection that Heyn[11] has shown by another method that the auxin of the roots of germinating *Vicia* seeds is also auxin-a. It might also be noted, however, that one experiment made with *non-sterile* roots of pea seedlings showed the presence of large amounts of indole acetic acid, presumably formed through

the action of microörganisms. Reserve must therefore be exercised in the interpretation of experiments dealing with the auxin relations of non-sterile roots.

The experimental procedure was as follows: A large amount (45 gms.) of roots which had been one week in culture and most of which were without tips (tips had been removed for the subsequent culture) was extracted with ether in the usual fashion, and the extract divided into 4 equal parts. One part was analyzed immediately for the determination of the amount of auxin originally present. The other three portions were placed in flasks and the ether removed completely by distillation. To one sample was then added 3 cc. of 5% HCl; to the second sample, 3 cc. of 0.5 normal NaOH and to the third sample 3 cc. of distilled water. The samples were then refluxed on a boiling water bath for 15 minutes, cooled, neutralized (slightly acid) and extracted with ether. This ether was then tested in the manner described above. The results of one experiment are summarized

TABLE 3

DETERMINATION OF THE NATURE OF AUXIN IN STERILE, ISOLATED ROOTS GROWING *in Vitro*. EXPT. NUMBER 80509

REFLUXED WITH	C	$(C \times I_1^{\circ} + O)$	V_{agar}	W	γ/KO.
HCl	2.6	7.7	0.6	$1/4 \times 44.6$	**0.420**
NaOH	+0.9	0	0.6	$1/4 \times 44.6$	**0**
H_2O	2.0	6.9	0.6	$1/4 \times 44.6$	**0.378**
not refluxed	2.3	7.5	1.0	$1/4 \times 44.6$	**0.681**

in table 3. It is of interest to note that the entire analysis was carried out with 30 millionths of a milligram "indole acetic acid equivalents." This corresponds, according to Kögl, Haagen-Smit and Erxleben,[12] to 15 millionths of a mg. of auxin-a.

Distribution of Auxin in the Root.—Table 4 shows that pea roots both at the end of the first culture, i.e., one week *in vitro*, and at the end of the second culture, i.e., two weeks *in vitro*, exhibit a very pronounced gradient of auxin concentration from the tip toward the base. This gradient is much steeper than that found by Thimann[7] for roots of *Avena* seedlings, but is similar to that found by Boysen-Jensen[1] for roots of germinating *Zea* and *Vicia* seeds.

Is Auxin Produced by Isolated Pea Roots in Vitro?—This question will be treated in detail in a later communication. However, the present experiments permit of a comparison of the total amount of auxin per average initial root tip (the 4 mm. tip cut from the germinating seed) with the total amount of auxin per average root after it has been two weeks in culture (and has hence been subcultured once). The average initial root tip (4 mm.) contains 137×10^{-6} gamma indole acetic acid equivalents. The total auxin content of the average root at the end of the second week is

TABLE 4

DISTRIBUTION OF AUXIN-a IN STERILE, ISOLATED ROOTS GROWN *in Vitro*, GAMMA "INDOLE ACETIC ACID EQUIVALENTS" PER KG. FRESH WEIGHT

EXPT. NUMBER	CULTURE	PART	LENGTH (AVERAGE)	C	$(C \times I_1° + O)$	V_{agar}	W	γ/KG.
80524	P I	tip	15 mm.	11.2	25.3	0.5	1.001	**12.7**
		middle	15 mm.	2.1	8.9	0.5	2.003	**2.22**
		base	24 mm.	15.9	34.0	0.5	7.609	**2.23**
80511	P II	tip	15 mm.	2.6	8.7	0.6	0.856	**6.10**
		middle	25 mm.	1.9	7.5	0.4	2.500	**1.20**
		base	25 mm.	1.1	6.0	0.5	8.900	**0.337**
80516	P II	tip	15 mm.	5.3	18.8	0.5	1.020	**9.2**
		middle	15 mm.	4.6	16.4	0.5	2.695	**3.04**
		base	20 mm.	3.2	12.0	0.5	8.490	**0.71**

70×10^{-6} gamma indole acetic acid equivalents. Thus although the root at the end of the second week does *contain* auxin, it appears to contain substantially less of this substance than does the initial tip.

Summary.—(1) Isolated *Pisum* roots cultivated *in vitro* were found to contain auxin for at least three weeks after the original tip was removed from the germinating seeds. (2) This auxin obtained from roots under sterile conditions has been shown to be auxin-a. (3) A steep auxin gradient was found in these isolated roots, the highest concentration being found in the tip. (4) Roots after two weeks' cultivation *in vitro* appear to contain less auxin than did the initial root tips.

[1] Boysen-Jensen, P., *Planta*, **19**, 354 (1933).

[2] Fiedler, H., *Zeit. Bot.*, **30**, 385 (1936).

[3] Nagao, M., *Sci. Rep. Tohoku Imp. Univ.*, **12**, 191 (1937).

[4] Bonner, J., and Addicott, F., *Bot. Gaz.*, **99**, 144 (1937).

[5] Pea seeds of the variety "Perfection," supplied by the Ferry-Morse Seed Co., San Francisco, were used. Seeds of the variety "Alaska" were used in a few experiments with substantially the same results.

[6] van Overbeek, J., *Proc. Nat. Acad. Sci.*, **24**, 42 (1938) and *Bot. Gaz.* (1938) (in press).

[7] Thimann, K. V., *Jour. Gen. Physiol.*, **18**, 23 (1934).

[8] van Overbeek, J., *Ibid.*, **20**, 283 (1936).

[9] Compare: Thimann, K. V., and Schneider, C. L., *Amer. Jour. Bot.*, **25**, 270 (1938).

[10] Kögl, F., Haagen-Smit, A., and Erxleben, H., *Zeit. Physiol. Chem.*, **228**, 104 (1934).

[11] Heyn, A. N. J., *Proc. Kon. Akad. Wetenschap., Amsterdam*, **38**, 1074 (1935).

[12] Kögl, F., Haagen-Smit, A., and Erxleben, H., *Zeit. Physiol. Chem.*, **228**, 90-(1934).

[13] Report of work carried out with the aid of the Works Progress Administration, Official Project Number, 465-03-3-342, Work Project N-9199.

THE MECHANISM OF HEARING AS REVEALED THROUGH EXPERIMENT ON THE MASKING EFFECT OF THERMAL NOISE

BY HARVEY FLETCHER

BELL TELEPHONE LABORATORIES

Read before the Academy April 26, 1938

Considerable information concerning the dynamical properties of the hearing mechanism can be obtained from physical measurements on audition. In fact, probably more precise information can be obtained by such measurements than from data obtained by animal experimentation, or from data on post mortem sections of human temporal bones.

It is well known that when a person is immersed in a noise his ability to hear other sounds is decreased. The noise is said to produce a masking effect. Before describing the experiments on the masking effect of thermal noise I will first describe the method of obtaining thermal noise and how it is quantitatively defined.

In an electrical conductor there is a statistical variation of the electrical potential difference between its two ends which is due to the thermal agitation of the atoms, including the electrons. This fluctuating voltage may be amplified by means of a vacuum tube amplifier. Such an electrical disturbance is called an electrical thermal noise. If this electrical thermal noise is sent through a telephone receiver, or a loud speaker, it is then converted into acoustical thermal noise. Such an acoustical thermal noise was used in the masking experiments discussed in this paper.

Let I_f be defined as the intensity per cycle of thermal noise using 10^{-16} watts* per square centimeter as a unit of intensity. If ΔI is the intensity due to the thermal noise in the band of frequencies between f and $f + \Delta f$, then

$$I_f = \frac{\Delta I}{\Delta f}. \tag{1}$$

The spectrum level B in decibels is defined by

$$B = 10 \log I_f. \tag{2}$$

In general I_f and B will vary with the frequency. The curve showing the variation of B is called a spectrogram of the noise.

Let us now examine more closely the relationship between the intensity of the noise and its masking effects. When a thermal noise having a given spectrogram is impressed upon the listener's ears it causes the hearing mechanism to vibrate some parts more and other parts less. These vibrations stimulate the nerve endings. The ear has a selective action for

sounds of different frequencies so that the amount of agitation or stimulation given any set of nerve endings will depend upon their position.

It is well known that the nerve endings responsible for auditory effects are located along the basilar membrane. According to the measurements of anatomists this membrane varies in width from 0.2 millimeter at the oval window end to 0.5 millimeter at the helicotrema end, and is about 30 millimeters long. It will be seen that it is about 100 times as long as it is wide. Therefore, a single coördinate x will define with sufficient accuracy the position of a patch of nerve endings. Then, if we take one per cent of the length it will contain a patch of nerve endings about as long as it is wide.

To make this concept more concrete, a spiral line having approximately the same shape as the human cochlea along which the basilar membrane runs is shown in figure 1. The numbers along the spiral line give the ap-

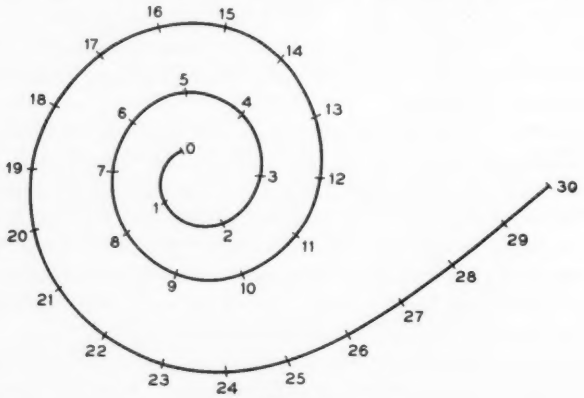


FIGURE 1

proximate distances in millimeters as you go from the helicotrema to the oval window. These dimensions vary in the ears of different persons. Also, the density of the nerve endings, that is, the number of endings per millimeter, is not accurately known. To avoid the necessity of using uncertain anatomical data, the position coördinate x will not be taken in millimeters from the helicotrema but as the per cent of total nerve endings that is passed over in going from the position of maximum stimulation for the lowest audible frequencies (the helicotrema) to a position designated by the coördinate x. The position coördinate thus defined is equal to zero at the helicotrema end and equal to 100 at the oval window end. For example, as will be shown later, the position x of maximum stimulation for a pure tone of frequency 5000 cycles per second is equal approximately to 75. This means that 75 per cent of the nerve endings are in the direction toward the helicotrema and 25 per cent in the direction toward the oval window.

Let us designate the distance in millimeters from the helicotrema as x'. There is then a simple relation between the position coördinate x and the distance in millimeters x' if we know the density σ, that is, the number of nerve endings per millimeter at each distance x'. This relation is given by

$$x = \frac{\int_0^{x'} \sigma \, dx'}{\int_0^{30} \sigma \, dx'}. \qquad (3)$$

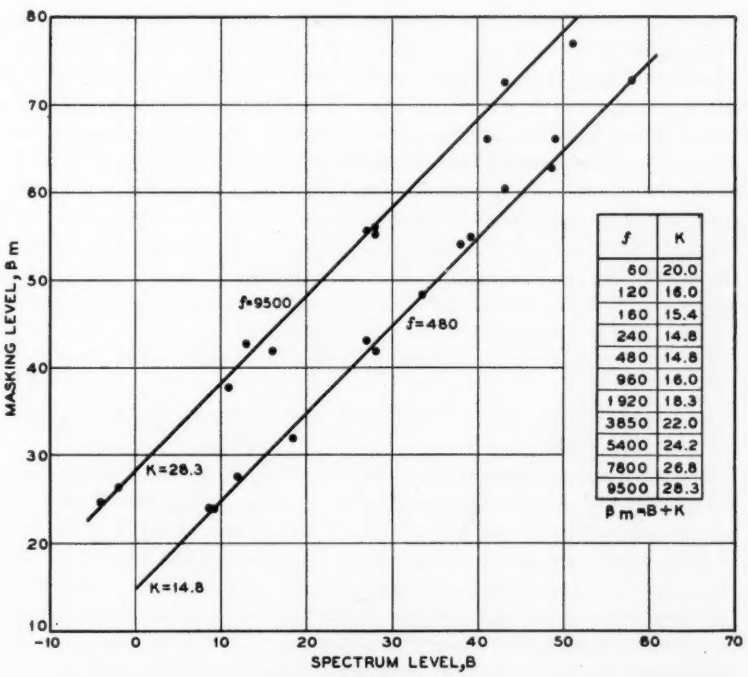


FIGURE 2

In our discussions we will use the coördinate x which can be determined directly from auditory experiments.

When a continuous noise is impressed upon the ear it produces a certain stimulation at the position x. The stimulating agent will be taken as the vibrational power acting upon the nerve endings. Let the amount of this power between positions x and $x + \Delta x$ be designated as ΔJ. Then the power J_x for one per cent of the nerve endings is given by

$$J_x = \frac{\Delta J}{\Delta x}. \tag{4}$$

The stimulation level S at any position x is defined by

$$S_x = 10 \log \frac{J_x}{J_0}, \tag{5}$$

where J_0 is the threshold stimulation. Since here we are dealing with a ratio of vibrational powers, the uncertainty of determining whether to use amplitude velocity or acceleration or any function of them as the stimulating agent does not arise. The value S_x can then be taken as the stimulation of the one per cent patch of nerve endings at the position x. This stimulating power can be spread over a small or a large patch of nerve endings and it will still produce just the threshold value. This is true because our experiments on loudness have shown that the nerve discharges near the threshold are proportional to the intensity of the sound.

Let the following experiments be performed. A broad band of thermal noise whose spectrum level B is known at each frequency is impressed upon the ear of an observer. While this noise is present, a pure tone of known frequency f is raised to the intensity I_m so that the observers just perceive its presence. The intensity level of this tone which is masked will be designated β_m and it is related to I_m by the equation

$$\beta_m = 10 \log I_m. \tag{6}$$

For a fixed frequency a set of values of β_m and B were obtained using different intensity levels of the noise.

The experimental apparatus and methods have been described elsewhere. A typical set of results is shown in figure 2 for two frequencies 9500 cycles per second and 480 cycles per second. The spectrum level B of the noise at each of these frequencies is plotted as abscissae and the intensity level of the pure tone just masked by the noise is plotted as ordinates. It was found that this relation was independent of the frequency width of the band as long as this exceeded a critical value ranging from 100 c. p. s. in the low frequencies to 1000 c. p. s. in the high frequencies. Points above $\beta_m = 80$ and below $\beta_m = 20$ are usually above the straight line which goes through the points between these levels. There is a reason for both of these departures which cannot be dealt with here. It is the straight portions of the curves which give us the information we want to use in this discussion. Since they are straight lines, equations of the form

$$\beta_m = B + K \tag{7}$$

will represent them, where K is a parameter varying with the frequency regions used. It is this variation that enables us to determine the relation

of the position of maximum stimulation x, to the frequency f of the impressed tone. Eleven frequency regions were tested and the results plotted on eleven straight lines like those of figure 2.† The resulting values of K are shown in figure 2 for the various frequencies used. The relation between the acoustic pattern and the corresponding stimulation pattern on the nerves is illustrated in figure 3. A 500-cycle band of noise between 500 and 1000 is spread into a wide stimulation pattern of 16 per cent of the nerve endings, while this same band width between 7500 and 8000 of the same acoustic intensity acts upon only one per cent of the nerve endings at position 88 as indicated. Consequently, one must raise the level of a pure tone in this high frequency region to a higher value to be perceived than if

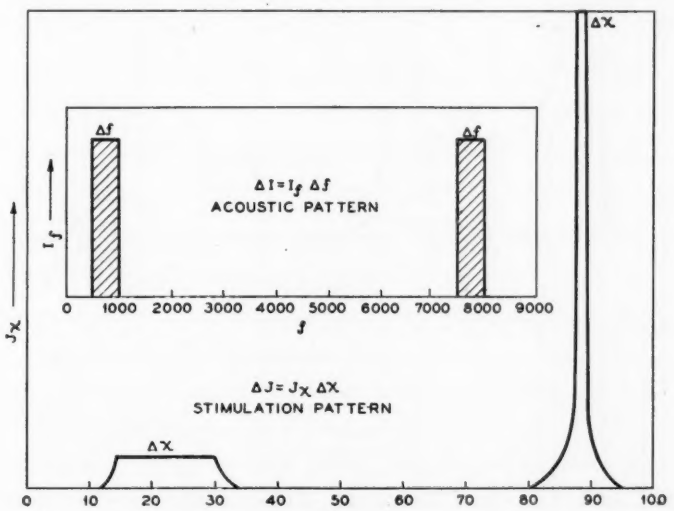


FIGURE 3

one were perceived in the low frequency region where the stimulation per nerve is not nearly so great. Conversely, if the masking level, compared to the spectrum level, is higher for the high frequency region than for the low frequency region, it shows that the frequencies are less spread out in the high and more spread out in the low frequency regions. For example, in the case illustrated the masking tone would be sixteen times greater for one than for the other.

Let us consider this relation in a quantitative way. The intensity ΔI in the thermal noise band between f and $f + \Delta f$ goes to stimulate mostly those nerve endings between x and $x + \Delta x$, where x corresponds to the position of maximum stimulation for a pure tone having a frequency f,

and $x + \Delta x$ to the position of maximum stimulation for a pure tone having a frequency of $f + \Delta f$. In other words, the band Δf located at the frequency position f will be chosen so that the power in this particular noise band is spread over the particular patch of nerves Δx located at the position x.

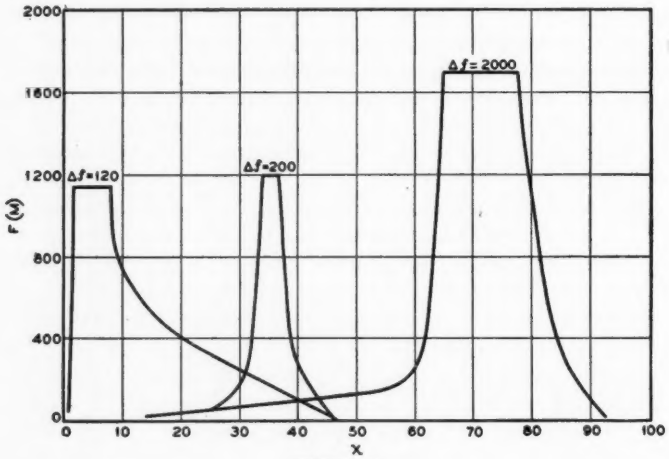


FIGURE 4

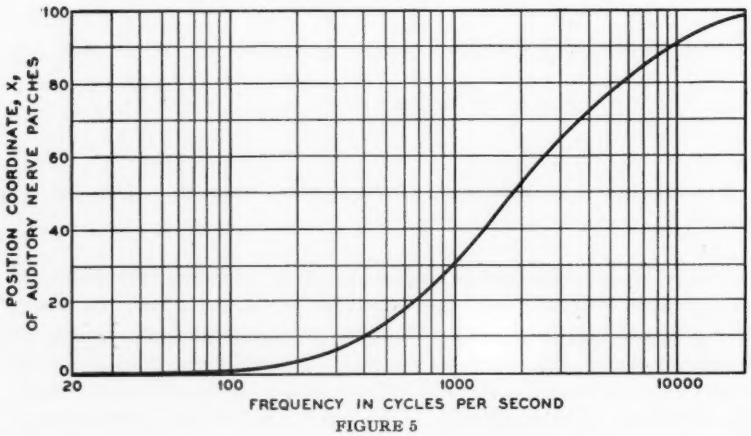


FIGURE 5

As illustrated in figure 3 the patches adjacent to Δx will also be stimulated if a single band Δf is impressed upon the ear. However, for any type of noise whose spectrum is not changing rapidly with frequency these adjacent patches will already be stimulated by the adjacent bands. For this type

of noise it is fairly accurate to assume that all the intensity in the band Δf goes to stimulate the nerve patch Δx. The response of the nerves stimulated by small bands of thermal noise has been calculated. The results of this calculation are shown in figure 4 for three different positions. It is seen that the ear is very selective with frequency and that the above assumption is a very good approximation.

Since the thermal noise band and also the masked tone are in the same frequency region, they will have approximately the same frequency discrimination produced by the electro-acoustical system generating the sounds and also by the transmission system in the ear. The acoustical intensity ΔI

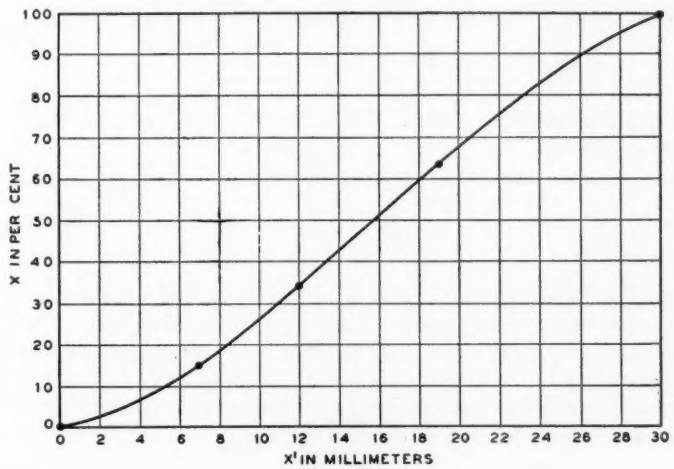


FIGURE 6

produces the stimulation ΔJ. The acoustical intensity I_m produces the stimulation J_m at the same nerve position x as for ΔJ. Therefore in the range where the system is linear

$$\frac{\Delta I}{\Delta J} = \frac{I_m}{J_m} = \frac{I_f \Delta f}{J_x \Delta x}. \tag{8}$$

If we consider Δf and Δx as differentials and integrate we have

$$x = \int_0^f \frac{I_f J_m}{I_m J_x}\, df. \tag{9}$$

It is now assumed that $\frac{J_m}{J_x}$ is a constant C independent of position x and consequently of the frequency f.

$$C = \frac{J_m}{J_x}. \tag{10}$$

Also, equation (9) must fulfil the condition that $x = 100$ when $f = \infty$. If these conditions are applied and the values of B and β_m from equations (2), (6) and (7), then equation (9) reduces to

$$x = C\int_0^f \frac{I_f}{I_m}\,df = C\int_0^f 10^{-K/10}df \tag{11}$$

where

$$C = \frac{100}{\int_0^\infty \frac{I_f}{I_m}\,df} = \frac{100}{\int 10^{-K/10}df}. \tag{12}$$

So we can substitute the values of K from figure 2 and integrate these equations graphically.

In the region where the system is linear

$$\frac{I_m}{I_0} = \frac{J_m}{J_0} \tag{13}$$

where I_0 is the threshold intensity of a band of thermal noise of small width located at the frequency position f corresponding to that of the tone which is masked, and J_0 the stimulation necessary for threshold at the position x corresponding to f. If we multiply the numerator and denominator of the left-hand side of this equation by J_x and then reduce the equation to decibels by taking 10 log of both sides, there results

$$\beta_m - \beta_0 = S + 10\log\frac{J_m}{J_x} = S + 10\log C. \tag{14}$$

The left-hand side of this equation is, by definition, the masking M. This shows that for a linear system the assumption that J_m/J_x is a constant is equivalent to assuming that for a constant masking there is a constant stimulation. In other words, the amount of masking M is a measure of the stimulation S and the difference between these two quantities is simply 10 log of the constant given by equation (10). If we express equation (7) in decibels and then rearrange the terms, there results

$$\beta_m = B + 10\log C + 10\log\frac{df}{dx}. \tag{15}$$

From this equation it is seen that the intensity level β_m of the masked tone can be calculated from the spectrum level B of the noise provided the relation between x and f is known.

Using the values of K shown in figure 3, equations (11) and (12) were integrated graphically. The value for C was found to be 1.1, or within the experimental error equal to unity. This means that when the stimulation J_m due to the tone being masked is equal to the stimulation J_x upon one per cent of the nerves then it will just be perceived by a typical observer. Also, this indicates that the masking M is directly equal to the stimulation S and may be considered a means of measuring it. The resulting values of f and x obtained from equations (11) and (12) are shown in the curve of figure 5. The relationship between f and x indicates that frequencies below about 150 cycles per second all have the position of maximum stimulation on the first one per cent patch of nerve endings. When the frequency of the stimulating tone reaches 1000 cycles per second the position of maximum stimulation has passed over approximately 30 per cent of the nerve endings.

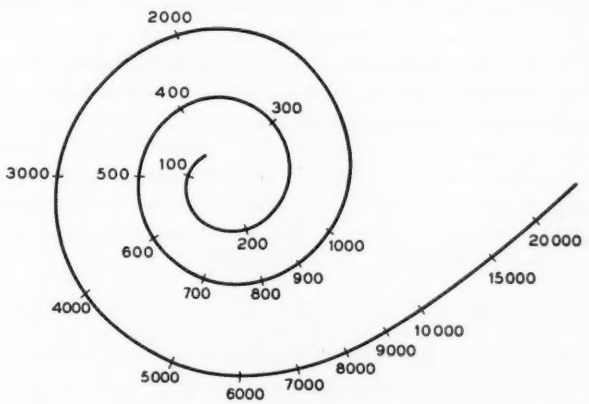


FIGURE 7

It will be remembered that the values of x refer to nerve patches in such a way that for equal intervals Δx there are an equal number of nerve endings. If the nerve endings are distributed uniformly along the basilar membrane then the values of x used in this discussion will correspond to one per cent of the total length of the basilar membrane. If, however, the nerve endings are not distributed uniformly, then the length dx must be stretched or contracted depending upon the nerve density being less or greater than the average. Let x' be the distance from the helicotrema in millimeters.

Guild‡ has made measurements of the number of ganglion cells along the basilar membrane. He divided the cochlea into four parts, namely (1) upper middle and apical, (2) lower middle, (3) upper basal, (4) lower basal.

He made a count of the total number of ganglion cells in each of these parts. They are given below in column 3 of table 1. Steinberg has esti-

TABLE 1

POSITIONS	x'	COUNT	x
Upper Middle plus apical	0–7	4,200	0–14.5
Lower Middle	7–12	5,600	14.5–33.8
Upper Basal	12–19	8,500	33.8–63.1
Lower Basal	19–30	10,700	63.1–100
Total	0–30	29,000	0–100

mated the distance in millimeters along the basilar membrane for each of these parts to be that given in the column under x'. The corresponding values of x are then easily calculated as the per cent of the total cells up to the position corresponding to x'. They are given in the last column.

It is seen that these data on the number of ganglion cells allow us to calculate only three points besides the two end-points. These values of x and x' are plotted on figure 6. A smooth curve passed through these points. Using this relation, then the values of x and f from figure 5 can be transferred to values of x' and f. In figure 7 this relation is plotted on a spiral having the dimensions shown in table 1. The positions given in this spiral agree with previous determinations within the accuracy of those determinations.

* All intensity values used in this paper are expressed by this same unit.

† I am indebted to Mr. W. A. Munson for doing this experimental work.

‡ Guild, Stacy R., *Acta Oto-Laryng.*, **17**, 207–245 (1932).

THE DIMENSIONLESS CONSTANTS OF PHYSICS

BY ARTHUR E. HAAS

UNIVERSITY OF NOTRE DAME

Communicated June 8, 1938

Physics appears to be characterized by several universal constants which are pure numbers. One is the ratio of the mass of the proton to the mass of the electron, i.e., $m_p/m = 1835$, another the ratio $e^2/(h\,c)$, where e is the fundamental charge, h Planck's constant and c the velocity of light. A third is the ratio $e^2/(G\,m_p\,m)$, where G represents the gravitational constant. An important fourth number, under the assumption of a finite uni-

verse, is given by the ratio M/m_p, where M denotes the total mass of the universe. It appears that a fifth constant, the ratio of the total number of neutrons to the total number of protons, should be introduced, this ratio being referred either to a static universe, or under the assumption of an expanding universe, to its initial equilibrium state.

It will be the task of this consideration to derive the result that the empirical constants of atomic physics yield for this ratio a value equal to unity to a high degree of approximation, provided that we can accept as correct the results of two earlier papers based on wave-mechanical deductions and published by Eddington and by Sitte and Glaser, respectively.

Eddington,[1] in 1931, derived the simple relation

$$R^2 = N_e a^2, \tag{1}$$

where R denotes the equilibrium radius of the universe, N_e the total number of electrons and a $(= e^2/(mc^2))$ the classical radius of the electron.

Sitte and Glaser[2] arrived at a formula which may be written in the following form

$$h/(M c) = R N_p^{-1/3} (N_p + N_e)^{-1}, \tag{2}$$

where N_p is the total number of protons; the existence of neutrons was not taken into account by Sitte and Glaser. Since, however, the only properties of protons and electrons which play a rôle in Sitte and Glaser's considerations are that the mass of the electron is insignificant in comparison with the mass of the proton, and that the universe as a whole is electrically neutral, equation (2) may be generalized as follows:

$$h/(M c) = R N^{-1} N'^{-1/3}, \tag{3}$$

where N is the total number of primordial particles of which N' are heavy in the sense that the mass of the other $(N - N')$ particles may be disregarded in comparison with their mass.[3]

If we denote the number of neutrons by N_n and remember that N_e equals N_p, we have

$$N = N_n + 2N_p, \qquad N' = N_n + N_p \qquad M = (N_n + N_p)\, m_p. \tag{4}$$

If we put

$$N_n = x N_p \tag{5}$$

we thus find

$$h/(m_p c) = R N_p^{-1/3} (1 + x)^{1/3} (2 + x)^{-1}. \tag{6}$$

By combining this relation with equation (1) and remembering the equality of N_p and N_e, we obtain

$$(2 + x)\,(1 + x)^{-1/2} = (m_p/m) \times e^2/(h\,c). \qquad (7)$$

The empirical value of the right-hand side is 2.13 and the solution of equation (7) is a value of x slightly above unity. It would just be equal to one if we could put the right-hand side of equation (7) equal to 2.12, thus diminishing its empirical value by half a per cent.

Thus, if the equations derived by Eddington and by Sitte and Glaser hold, we arrive at the conclusion that in the state of equilibrium the number of neutrons nearly equals the number of protons. On the other hand, a relation, first pointed out by the author,[4] which connects purely atomic constants and which is fulfilled to within an error of about half a per cent, i.e.,

$$m_p/m \times e^2/(h\,c) = 3/\sqrt{2} \qquad (8)$$

may be derived from the formulae of Eddington and Sitte and Glaser by assuming the equality of the numbers of neutrons and protons in the equilibrium state.

[1] A. S. Eddington, *Proc. Roy. Soc. London*, **A135**, 605 (1931).
[2] K. Sitte and E. Glaser, *Zeitschr. Physik*, **88**, 103 (1934).
[3] Concerning the details, cf. the paper by Sitte and Glaser.
[4] A. E. Haas, *Science*, June (1938): The classical radius of the electron is related to the Compton wave-length of the proton as 3 to $\sqrt{2}$.

ON THE RELATIVE CONTRIBUTIONS OF NATURE AND NURTURE TO AVERAGE GROUP DIFFERENCES IN INTELLIGENCE

BY BARBARA S. BURKS

CARNEGIE INSTITUTION OF WASHINGTON, COLD SPRING HARBOR

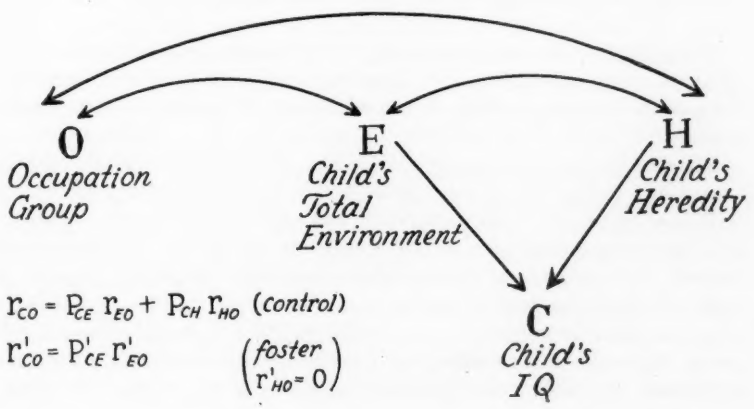
Communicated June 13, 1938

It has become a more or less accepted commonplace that environmental differences, although having a demonstrable influence upon individual differences in IQ, are less potent than natural differences under the conditions ordinarily met in our urban culture. No wholly satisfactory quantitative estimate of the relative rôles of nature and nurture has yet been possible, but various estimates agree in placing the contribution of nurture under 50 per cent, and probably considerably under. (See references 1 to 5.)*

Far less satisfactory is the present position of the problem of average socio-economic *group* differences in intelligence—in fact it is only in the last few years that it has been generally recognized and discussed as a separate problem requiring its own techniques for solution. There is no simple correspondence between the contributions of nature and nurture to group and individual differences, but the same types of data are crucial for both problems. The writer has drawn upon two sources of data applicable to the problem of average group differences in IQ with respect to father's occupation—her previous study conducted at Stanford University of the IQ's of foster children and "own" children in relation to parental intelligence and home background, and the more recent study by Leahy at University of Minnesota dealing with the same type of material.

The comparisons involved are unusually straightforward, for it can be shown that the difference in mean IQ of "own" children grouped according to father's occupation is composed of two additive heredity and environment factors, the latter being given by the corresponding difference in group means of foster children. Wright has kindly furnished a proof, which depends upon the use of path coefficients, as follows:

Child's IQ can be represented as completely determined by the two factors—heredity (i.e., the *child's* genetic constitution) and total environment, which may be (and undoubtedly are) more or less correlated with each other. Occupational status of father is clearly correlated with the child's total environment. The increased differences in the control data indicate that it is also correlated with the child's heredity in the controls. The reasons (involving father's intelligence) need not be represented. The following diagram represents these essential points:



The observed differences in IQ in relation to given differences in occupation group are of the nature of regression coefficients.

$$b_{CO} = r_{CO}\frac{\sigma_c}{\sigma_o} = (p_{CE}r_{EO} + p_{CH}r_{HO})\frac{\sigma_c}{\sigma_o} \text{ (control)},$$

$$b'_{CO} = r'_{CO}\frac{\sigma_c'}{\sigma_o'} = (p'_{CE}r'_{EO})\frac{\sigma_c'}{\sigma_o'} \qquad \text{(foster)}.$$

The partial regression coefficients measuring the concrete effects of H and E on C should be the same in foster and control data in spite of differences in correlations, path coefficients or standard deviations.

$$p_{CE}\frac{\sigma_e}{\sigma_o} = p'_{CE}\frac{\sigma_e'}{\sigma_o'}, \qquad p_{CH}\frac{\sigma_c}{\sigma_o} = p'_{CH}\frac{\sigma_e'}{\sigma_o'}.$$

If now we assume that the correlation between total environment and occupation group is the same in the two bodies of data but that there is no correlation between child's heredity and occupation group in the foster data (no effective selection of children):

$$r_{EO} = r'_{EO}, \qquad r'_{HO} = 0,$$

$$b_{CO} = p_{CE}r_{EO}\frac{\sigma_e}{\sigma_o} + p_{CH}r_{HO}\frac{\sigma_c}{\sigma_o} \qquad \text{(control)},$$

where $$p_{CE}r_{EO}\frac{\sigma_e}{\sigma_o} = b'_{CO} \text{ given by the foster data.}$$

Thus the difference in the controls can properly be analyzed into two additive portions tracing through the correlation of occupation group with child's environment, which is the same as the total difference in the foster data, and tracing through the correlation with child's heredity.

The published Minnesota study provides the needed tabulations for occupational group comparisons. It was necessary to go back to the original data of the Stanford study and tabulate them according to a similar scheme.†

The results are shown in tabular form. Table 1 contains the group means and dispersions of intelligence test scores; those of the parents as well as of the children are included by way of additional interest. Table 2 contains derived estimates of the relative contributions of nature and nurture to occupational group differences. The "nurture" column of table 2 is simply the ratio (in per cent) of group difference in foster children to group difference in control "own" children. The "nature" column is 100 minus this ratio, or the ratio of increment of control difference to control difference. In table 3 are presented estimates of the relative contribu-

tions of nature and nurture based upon the total data of the Stanford and Minnesota studies, singly and in combination. Sampling errors of these estimates are also included.

Two methods, giving virtually the same results, were used for obtaining combined estimates of the nature and nurture contributions (table 3).

1. The occupational group differences shown in table 2 were summed for the control and foster groups separately, and the ratio of the foster sum to the control sum was computed. This procedure is sufficiently ac-

TABLE 1

MEANS AND DISPERSIONS OF INTELLIGENCE SCORES BY OCCUPATIONAL GROUP

	STANFORD STUDY OCCUPATION OF FATHER (OR FOSTER FATHER)				MINNESOTA STUDY OCCUPATION OF FATHER (OR FOSTER FATHER)				
	PROFESS. I.	HIGHER BUS., SEMI-PROF. II.	LOWER BUS. III.	SKILLED LABOR IV.	PROFESS. I.	BUS. MGR. II.	SKILLED TRADES & CLERICAL III.	SEMI-SKILLED IV.	SLT. SKILLED & DAY LABOR V.
Foster children									
Mean (IQ)	109.1	108.6	108.0	104.6	112.6	111.6	110.6	109.4	107.8
S. D. (IQ)	17.2	14.5	14.3	16.7	11.8	10.9	14.2	11.8	13.6
No.	32.0	47.0	41.0	43.0	43.0	38.0	44.0	45.0	24.0
Control children									
Mean (IQ)	118.7	118.5	115.5	106.1	118.6	117.6	106.9	101.1	102.1
S. D. (IQ)	15.4	12.2	18.6	12.4	12.6	15.6	14.3	12.5	11.0
No.	18.0	33.0	27.0	18.0	40.0	42.0	43.0	46.0	23.0
Foster parents*									
Mean	221.8	207.3	201.2	184.7	59.6	59.6	49.6	39.7	38.4
S. D.	22.6	30.8	29.7	30.3	8.0	6.7	11.9	12.3	11.2
No.	24.0	40.0	34.0	34.0	...	...	...	...	...
Control parents*									
Mean	221.6	221.8	192.0	176.2	64.6	57.1	51.8	44.0	38.3
S. D.	24.4	30.4	33.4	31.6	5.4	10.0	11.5	11.5	9.0
No.	18.0	32.0	27.0	18.0	...	...	...	...	...

* In the case of the Stanford study, data are for Stanford-Binet mental age in months of foster fathers and control fathers. In the case of the Minnesota study, data are for mid-foster parent and mid-parent point score on the Otis Test of Mental Ability.

curate for an over-all appraisal when the population numbers and standard deviations of the sub-groups do not differ in an extreme manner. The sampling errors of the estimates thus obtained, however, are difficult to determine because of the lack of independence of the group differences entering the sums.

2. Using the relation,‡

$$\frac{\overline{x_F - \bar{x}_F}}{\sigma_F} = r\,\frac{x_C - \bar{x}_C}{\sigma_C} \qquad (1)$$

and assuming a true r of unity (i.e., a constant proportional effect upon IQ of nurture and nature in the small range of IQ levels with which we are concerned), we may estimate the proportional contributions by the ratio**

$$R = \frac{\sigma_F}{\sigma_C}. \tag{2}$$

The sampling variance of R is found by squaring and averaging logarithmic differentials, viz.,

$$V_o(R) = R^2\left[\frac{V_o(\sigma_F)}{\sigma_F{}^2} + \frac{V_o(\sigma_C)}{\sigma_C{}^2}\right]. \tag{3}$$

σ_F, σ_C represent the dispersions of sets of scores in which each score is drawn from a unique universe of given central tendency and sampling

TABLE 2

ESTIMATES OF THE RELATIVE CONTRIBUTION OF NATURE AND NURTURE TO DIFFERENCES IN MEAN INTELLIGENCE SCORE OF CHILDREN GROUPED ACCORDING TO FATHER'S OCCUPATION

	STANFORD STUDY					MINNESOTA STUDY				
GROUPS COMPARED	CONTROL	FOSTER	CONTROL MINUS FOSTER	CONTRIB. OF NURTURE	CONTRIB. OF NATURE	CONTROL	FOSTER	CONTROL MINUS FOSTER	CONTRIB. OF NURTURE	CONTRIB. OF NATURE
I–II	0.2	0.5	..	..	..	1.0	1.0	..	..	..
I–III	3.2	1.1	2.1	34.4	65.6	11.7	2.0	9.7	17.1	82.9
I–IV	12.6	4.5	8.1	35.8	64.2	17.5	3.2	14.3	18.3	81.7
I–V	..	..	..	..	..	16.5	4.8	11.7	29.1	70.9
II–III	3.0	0.6	2.4	20.0	80.0	10.7	1.0	9.7	9.3	90.7
II–IV	12.4	4.0	8.4	32.3	67.7	16.5	2.2	14.3	13.3	86.7
II–V	..	..	..	..	..	15.5	3.8	11.7	24.5	75.5
III–IV	9.4	3.4	6.0	36.2	63.8	5.8	1.2	4.6	21.7	79.3
III–V	..	..	..	..	..	4.8	2.8	2.0	58.4	41.6
IV–V	..	..	..	..	..	−1.0	1.6	..	..	..

fluctuation. Hence their sampling variances (to be used in formula 3) cannot be calculated by the usual formula. A formula for $V_o(\sigma_F)$, $V_o(\sigma_C)$ may be derived as follows:

$$\sigma^2 = S\frac{(x_i - \bar{x})^2}{n - 1} \tag{4}$$

$$= \frac{(x_1 - \bar{x})^2 + \ldots\ldots (x_n - \bar{x})^2}{n - 1}.$$

Taking differentials, squaring and averaging,

$$V_o(\sigma) = S\frac{[(x_i - \bar{x})^2\,(V_o(x_i) + V_o(\bar{x}) - 2/nV_o(x_i))]}{\sigma^2(n - 1)^2}$$

$[V_o(x_i) = \sigma^2 x_i/n_i$, obtainable from table 1].

The difference in estimated contributions of nature and nurture yielded by the Stanford study ($<2/3, >1/3$) and the Minnesota study ($>3/4$, $<1/4$) may be due to sampling error alone, although examination of the slope of the regression of foster means upon control means in the two studies suggests that the estimate of the potency of nurture is rather consistently lower in the Minnesota study than in the Stanford study. This may perhaps be accounted for by the fact that there was less opportunity for "selective placement" in the Minnesota foster children, who were limited to those placed in adoptive homes under 6 months of age, than in the California foster children who were placed up to 12 months of age.

TABLE 3

ESTIMATES OF THE RELATIVE CONTRIBUTION OF NATURE AND NURTURE BASED UPON TOTAL DATA, WITH TESTS OF SIGNIFICANCE

	STANFORD STUDY	MINNESOTA STUDY
Unweighted sum of control group differences	40.8	99.0
Unweighted sum of foster group differences	14.1	23.6
Estimated contribution of nurture $\left(\frac{\text{foster grp. diff.}}{\text{control grp. diff.}}\right)$	**0.345**	**0.238**
Estimated contribution of nature (1-nurture contrib.)	**0.655**	**0.762**
Dispersion of control group means (σ_C)	5.92	8.37
Dispersion of foster group means (σ_F)	2.03	1.87
Estimated contribution of nurture ($R = \sigma_F/\sigma_C$)	**0.344**	**0.224**
Estimated contribution of nature ($1 - R$)	**0.656**	**0.776**
Sampling variance of R ($V_o(R)$)	0.054	0.017
Sampling error of R ($\sqrt{V_o(R)}$)	**0.232**	**0.131**
Information ($1/V_o(R)$)	18.59	58.82

Combined $\bar{R}$ (weighted according to information)	**0.253**
$1 - \bar{R}$	**0.747**
$V_o(\bar{R})$	0.013
Sampling error ($\sqrt{V_o(\bar{R})}$)	**0.114**

Combining the estimates in the two studies according to the amount of information yielded by each (inversely as their sampling variances), we arrive at an estimated 3/4, 1/4 as the relative contributions of nature and nurture, with approximately even chances that the contribution of nurture is in truth between 18 and 33 per cent.

Finally, it may be pointed out that differences in mean intelligence scores of the parents according to occupational group might be expected to derive from natural differences in a higher proportion than do those of their offspring, since intelligence is one of the components that enters directly into

the selection of an occupation, or the selection of a person by an occupation. This truism is borne out by the higher regression of intelligence on occupation in the parent groups than in the offspring groups.

* Reference 3 contains quantitative estimates of the contributions of nature and nurture which have been strongly criticized. However, the simple correlation, 0.67, between the intelligence scores of identical twins reared apart—which would rise even higher if corrected for attenuation, and for the restricted range of talent—is in itself weighty evidence for the predominant influence of natural inheritance.

† To avoid the slightest possibility of bias, the classification of fathers' occupations from the Stanford data was made "blind," i.e., with no knowledge as to the intelligence of the fathers, mothers, their children or foster children.

‡ In the formulae which follow, x, $\bar{x}$ and σ refer to the occupational group means, the mean of the means and the standard deviation of the means, respectively.

** This formula neglects a small error factor involving the magnitude of the obtained σ's in relation to the true σ's [i.e., $\sigma_\infty^2 = \sigma^2(r)$, where r is a reliability coefficient].

[1] Burks, B. S., *27th Yearbook Nat. Soc. Stud. Educ.*, Part I, 219–316 (1928).

[2] Leahy, A. M., *Genet. Psychol. Monog.*, **17**, 235–308 (1935).

[3] Newman, H. H., Freeman, F. N., and Holzinger, K. J., *Twins*, Univ. Chicago Press, pp. xvi + 369 (1937).

[4] Willoughby, R. R., *27th Yearbook Nat. Soc. Stud. Educ.*, Part I, 55–59 (1928).

[5] Wright, S., *Jour. Amer. Stat. Assoc. Suppl.*, **26**, 155–163 (1931).

A METAGALACTIC DENSITY GRADIENT

BY HARLOW SHAPLEY

HARVARD COLLEGE OBSERVATORY

Communicated June 14, 1938

1. In a discussion of the evidence bearing on the isotropic distribution of galaxies it was shown four years ago that at a distance of about 10^8 light-years to the north of the galactic plane the density is thirty or more per cent greater than at the same distance to the south.[1] Several different ways of discussing the extensive observational material yielded the higher density in the north. Similar inequalities were found to be present also at shorter distances, but beyond 10^8 light-years both the Harvard and the Mount Wilson data suggest tentatively the disappearance of the north-south inequality.

Quantitatively the north-south difference is not closely determined by the early work because the nebular counts were made in relatively small sample areas; but the existence of the difference is unquestionable, as is also the occurrence of non-uniformity in nebular distribution arising from the metagalactic clouds.[2] These well-established large-scale inequalities have been pretty generally ignored in discussions of the expanding uni-

verse; the assumptions of isotropy and large-scale uniformity have persisted, leading of late to somewhat remarkable deductions.

From surveys with reflecting telescopes Hubble has found a radial density gradient which, over an interval of 2.5×10^8 light-years, amounts to a density change of something less than twenty per cent.[3] To eradicate this ap-

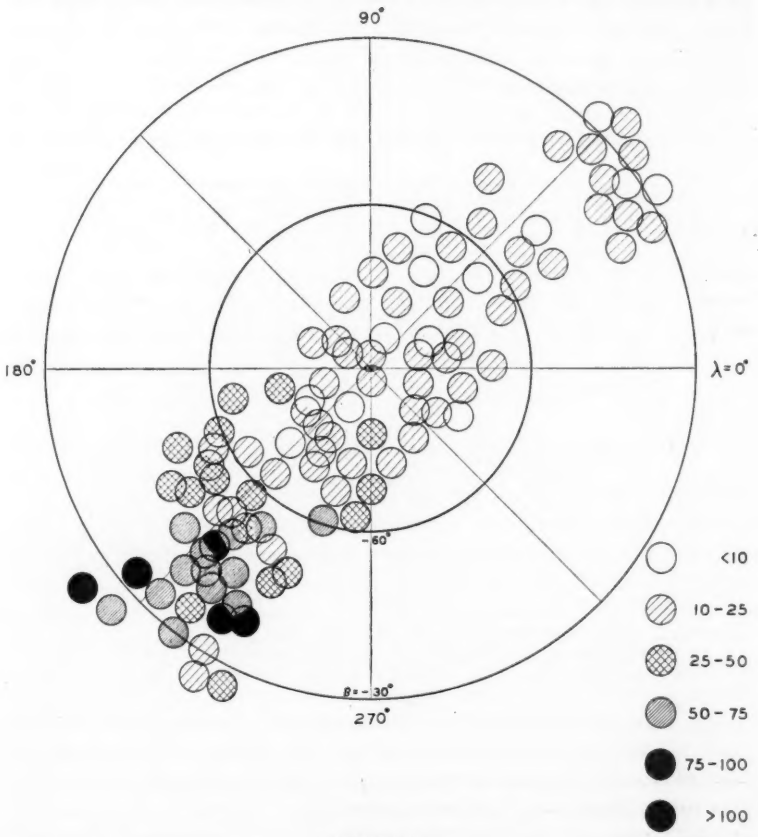


FIGURE 1

The density distribution in a thirty-degree zone across the south galactic pole.

parent increase in density with distance and restore nebular distribution to essential uniformity, he suggests the abandonment of the interpretation of red-shift as velocity of recession and the abandonment, therefore, of the hypothesis of the expanding universe, introducing in its place some new principle to account for the observed red-shift. But the evidence for

a radial gradient is not very strong. It can be readily shown that if the Mount Wilson surveys are analyzed separately for the two galactic hemispheres the gradient to the north is inappreciable.

In a recent discussion of the distribution of over seventy-five thousand galaxies in the south galactic polar cap[4] we have shown, in another way, that the accurate determination of a radial gradient is not yet possible because of the large density irregularities that exist up to distances of 10^8 light-years, if not throughout all attainable space. If, combining the Mount Wilson and Harvard counts of galaxies, we use as a standard for our density calculation the mean value obtained from the census in the first (northwest) longitude quadrant of the polar cap, we find that the density *increases*

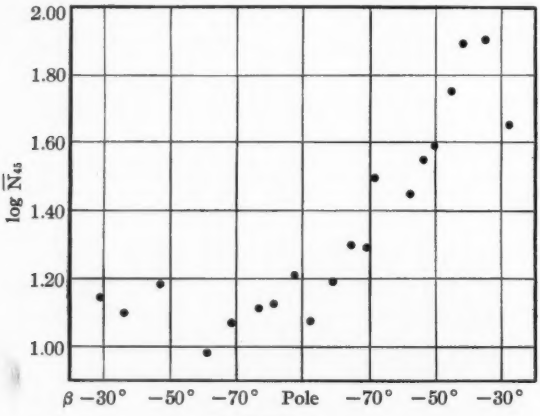


FIGURE 2

The metagalactic gradient as shown by a survey using the nine central square degrees of one hundred plates. Numbers of galaxies have been reduced to a common magnitude limit.

conspicuously with distance; if we use as standard the comparable material from the third quadrant, the density *decreases* slightly. These quadrants contain over 39,000 observed galaxies, and the determination of the difference in the density therefore has high weight.

2. The survey of the south galactic cap provides evidence of a long-distance transverse gradient or inequality in metagalactic density[4] that is as pronounced as the north-south inequality referred to above. It is more securely established by the observations because of the greater amount of material involved. Since this progressive inequality observed in the south galactic cap is across the line of sight, its measurement is free of first order difficulties with magnitude scales. The radial gradient suggested by the Mount Wilson surveys directly assumes a correct magnitude scale, and

disappears, according to Hubble,[3] if the scale is too restricted by 0.12 between magnitudes 18.5 and 21.0. The north-south inequalities found from the Harvard surveys four years ago involve the inter-comparison of frequencies in opposite regions, and such nebular counts are also moderately free of the effects of scale errors in the magnitude system.

3. The work on the south galactic cap (galactic latitudes $-55°$ to $-90°$) has now been extended in order to explore further the progressive though somewhat irregular increase of nebular frequency as the survey crosses the south galactic pole from the northwest to the southeast. The increase was grossly shown when we found in the four quadrants the following numbers of galaxies,* to the average magnitude 18.2 (number of plates in parentheses):

Northwest	10,800 (18)	Southwest	22,800 (21)
Northeast	19,000 (18)	Southeast	23,000 (23)

Reducing the counts to a common magnitude and using only results from the inner nine square degrees on each plate, we obtain the following values for the number per square degree:

Northwest	31.87	Southwest	51.10
Northeast	54.17	Southeast	66.54

The richest quadrant, on the average, is twice as rich as the poorest; the transverse distance involved is of the order of 10^8 light years.

4. The manner in which the survey has been extended is most clearly indicated by the polar diagram in figure 1. The south galactic pole is at the center; galactic latitudes and longitudes form the coördinate system. In a zone thirty degrees wide across the south galactic polar cap, centrally aligned on the longitude circle 45°, 225°, the positions are plotted of one hundred survey plates (each of three hours' exposure with the Bruce telescope). The frequency of galaxies is roughly indicated by the shading. The area of each circle is approximately twenty-five square degrees—the same as that covered effectively on the sky by a Bruce plate.

The diagram shows that the density continues to increase to the southeast, beyond the limits of the earlier survey.[4] Whether the maximum has been reached at latitude $-35°$ (right ascension 5^h, declination $-60°$), before the absorption of the Milky Way system makes itself appreciably felt, cannot yet be determined. The observed falling-off in density beyond the maximum is probably a feature of metagalactic structure in this region, but may be also in part caused by outlying Milky Way absorption, which has

* The objects lying outside the twenty-five square degrees on each of the eighty plates are not included. They approximately balance in number the objects appearing twice in overlapping of plates for which correction has not been made in the summation above.

been shown in a study of the south equatorial polar cap to be widespread in this part of the sky.[2]

In table 1 mean values, reduced to the convenient magnitude limit 17.9, are given for the results from the central nine square degrees of the plates, and also for the surrounding sixteen square degrees. Each mean includes the results of five plates, and therefore forty-five square degrees and eighty square degrees, respectively, are represented by each entry and by the plotted points of figures 2 and 3. The last column of the table gives for each group of five plates the total number of galaxies actually observed within the twenty-five square degrees.

TABLE 1

POSITIONS AND AVERAGE NUMBERS OF GALAXIES PER SQUARE DEGREE

GALACTIC		LOGARITHMS		TOTAL NUMBER
LONG.	LAT.	$\bar{N}_{45}$	$\bar{N}_{80}$	OF GALAXIES
45°	−29°	1.14	0.88	3,630
	−36	1.10	0.85	4,353
	−47	1.18	1.00	3,788
	−61	0.99	0.87	2,773
	−68.5	1.07	0.92	3,475
	−76.5	1.12	0.90	3,440
	−81	1.13	0.91	5,992
	−87	1.21	1.08	4,789
225	−88	1.08	0.88	4,570
	−81	1.20	0.95	4,648
	−75.5	1.30	1.10	5,650
	−71	1.30	1.08	5,846
	−68.5	1.50	1.29	7,582
	−58	1.45	1.35	4,363
	−54	1.55	1.38	4,820
	−50.5	1.60	1.47	4,918
	−45.5	1.76	1.58	6,669
	−41.5	1.90	1.71	6,557
	−35	1.91	1.70	5,706
	−28	1.66	1.48	3,978
			Total	97,547

So much area and so many objects are included in each mean that they no doubt smooth out large local irregularities. But the plots are given here chiefly to show the large-scale non-uniformity that stretches over 125 degrees of the southern sky. The completion of the eighteenth magnitude survey for the southern hemisphere will permit more detailed description of the nebular distribution; but as it stands, we see a conspicuous and steady rise in the frequency from $\bar{N}_{45} = 10$, at about latitude $-60°$ in the northwest quadrant, to $\bar{N}_{45} = 80$, at about latitude $-35°$ in the southeast quadrant.

The distance of the objects that chiefly establish the mean values is approximately 1.3×10^8 light-years. From the region of minimum frequency to that of maximum frequency is therefore about 2×10^8 light-years —a transverse distance comparable to that over which Hubble found an apparent radial gradient. Since we find here the frequency increasing by

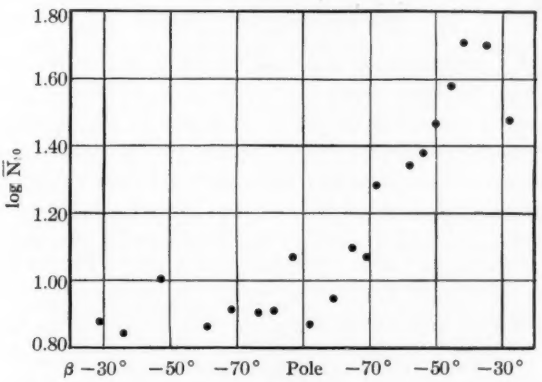


FIGURE 3

The metagalactic gradient as shown by a survey using the sixteen square degrees surrounding the central 9-square on a hundred plates. Galaxies only to a limit $0^m.3$ brighter than that for figure 2 are represented by this density curve.

several hundred per cent, it would appear reasonable to accept a twenty per cent radial density change as a minor detail of metagalactic structure, probably not associated significantly with the interpretation of the redshift or with space curvature.

[1] *Harv. Bull.*, **894** (1934).

[2] *Harv. Ann.*, **105**, Tercentenary Paper No. 8 (1937); see also *Harv. Ann.*, **88**, No. 5 (1935).

[3] *Mon. Not. R. A. S.*, **97**, 508 (1937).

[4] These PROCEEDINGS, **24**, 148 (1938); *Harv. Circ.*, **423** (1937).

A TARSIID PRIMATE AND A MIXODECTID FROM THE POWAY EOCENE, CALIFORNIA

BY CHESTER STOCK

BALCH GRADUATE SCHOOL OF THE GEOLOGICAL SCIENCES, CALIFORNIA INSTITUTE OF TECHNOLOGY

Communicated June 7, 1938

Introduction.—Following the discovery and description of a titanothere[1] in the Poway sands of San Diego County, continued excavation in this important Eocene horizon has produced small lots of mammalian remains. One of these included specimens of a tarsiid primate and a mixodectid. Worthy of mention is the fact that the former represents a third member of the Tarsiidae to be discovered in the early Tertiary of the Pacific Coast region. Since the Poway fauna possesses considerable significance in any attempt to correlate the later Eocene horizons of the Pacific Coast with those of the Cordilleran Province, it seems desirable to place on record these new mammals from the Poway.

Yumanius woodringi, n. gen. and n. sp.

Type Specimen.—Right maxillary fragment with $M\underline{1}$ and $M\underline{2}$, No. 2233, Calif. Inst. Tech. Vert. Pale. Coll., Plate 1, figure 1.

Paratypes.—Fragment of right ramus with $M\overline{1}$–$M\overline{3}$, No. 2234, Plate 1, figures 2, 2*a* and ramal fragment with $M\overline{2}$, $M\overline{3}$, No. 2235, Plate 1, figures 3, 3*a*.

Locality.—White sandstones associated with the Poway conglomerate and exposed on west bank of San Diego River, approximately one-quarter mile north and east of San Diego Mission; C. I. T. Vert. Pale., Loc. 249.

Generic and Specific Characters.—Upper molars differ from those of *Euryacodon lepidus* in possessing well developed and clearly defined hypocone or postero-internal cusp. Intermediate cusps also well developed. A second small cusp, comparable in size to that of the metaconule is situated between the latter and the base of the protocone. $M\underline{2}$ smaller than that in *Dyseolemur sylvestris* and hypocone, in contrast to that in the latter, more like a cingular cusp.

Lower molars 2 and 3 with trigonid portion of crown compressed anteroposteriorly and paraconid considerably reduced in size, more so than in *Euryacodon*. $M\overline{3}$ with broader posterior rim to heel. Distinctly different from *Dyseolemur* in reduction in size of trigonids in posterior molars and in absence of metastylid. I take pleasure in naming the species for my former colleague, Dr. Wendell P. Woodring of the U. S. Geological Survey.

Comparisons.—The upper molar teeth of *Yumanius woodringi* exhibit a cingulum on the outer, anterior and posterior sides of the crowns but the

basal ledge is lacking on the inner side. The small cuspule shown by Wortman[2] as situated at the inner base of the protocone in $M\underline{2}$ of *Euryacodon lepidus* is absent in the comparable tooth of *Y. woodringi*, but a slight development of the cingulum does occur in the second molar at the antero-internal base of the cusp. In the type specimen of *E. lepidus*, No. 11813 Y. P. M., the enamel of the crowns of the upper molars is smooth, the postero-internal cusp is not clearly indicated and the intermediate cuspules are small. In the molars of *Yumanius*, the postero-internal cusp shows pronounced development and the structural features of the crown become more complicated by the addition of a small cusp between metaconule and protocone. In addition the anterior ridge of the protocone, directed toward the protoconule, is more strongly formed in *Yumanius* than in *Euryacodon*.

The molars are unfortunately the only teeth preserved of the lower dentition. These resemble most closely the comparable teeth in *Euryacodon*. The enamel of the crowns is wrinkled, not smooth as in *Omomys;* the teeth are small, the paraconid while of normal size in $M\underline{1}$ becomes reduced to vestigial proportions or to the point of disappearance and the trigonid parts of the teeth are compressed anteroposteriorly. This compression of the trigonid portion of the crown is greater in the Poway genus than in *Euryacodon* or *Anaptomorphus*. In $M\underline{3}$ the posterior rim of the heel is broad and the end of the crown is not pointed as in *Euryacodon*. While no distinct metastylid is present as in *Dyseolemur* and *Washakius*, the posteriorly directed wing or ridge of the metaconid is extended in fore and aft line and is compressed transversely in *Yumanius*.

In the type of *Anaptomorphus aemulus* Cope, No. 5010 A. M. N. H., the teeth are smaller than in *Yumanius*. In $M\underline{1}$ of both forms the paraconid is well developed. This cusp becomes vestigial in $M\underline{2}$, but its reduction and the anteroposterior compression of the trigonid is greater in *Yumanius*. In the lower molars of the Bridger genus the external cingulum is not so well developed as in the San Diego specimens.

Discussion.—The upper and lower jaw specimens with teeth herein referred to the new genus *Yumanius* were found at one locality in the Poway but were not directly associated. The view that the type and paratypes belong to two distinct tarsiid genera cannot be ignored, although apparent absence of evidence other than that of fortuitous occurrence makes this possibility a seemingly remote one. Presence of this material in the Poway gives strength to the belief that Wortman's reference of the three lower jaw fragments of a tarsiid from the Bridger to *Euryacodon lepidus* is correct. It follows, as Matthew[3] pointed out, that *Anaptomorphus* and *Euryacodon* are probably identical. Among the several tarsiid genera recorded from the Bridger middle Eocene the Poway type is most closely related to the *Euryacodon-Anaptomorphus* stock. *Yumanius* appears to

have carried the line a stage farther and its presence at the San Diego locality suggests at least a post-Bridger age for the Poway. Curiously, *Y. woodringi* is more closely related to the Bridger species *E. lepidus* than to the Sespe type, *Dyseolemur pacificus*.

Microsyops kratos, n. sp.

Type Specimen.—A left ramus with $Dp\overline{3}$, $P\overline{4}$–$M\overline{3}$ inclusive and root fragments of the anterior premolars and canine, No. 2232, C. I. T. Vert. Pale. Coll., Plate 1, figures 4, 4*a*.

Locality.—Poway sandstones and conglomerates; C. I. T. Vert. Pale., Locality 249.

Specific Characters.—Differing from *Microsyops elegans* and *M. annectens* most noticeably in size. Smaller than *Craseops sylvestris*, but with lower molars, relative to size of jaw, larger than in latter species.

Description and Comparison.—This is the largest species of *Microsyops* so far recorded, being distinctly larger than *M. elegans* and *M. annectens* and resembling in size the species of *Craseops* recorded from the upper Eocene stage of the Sespe of Southern California. $Dp\overline{3}$ is a two-rooted tooth with simple crown. The latter is triangular in cross-section with apex placed forward. A downwardly directed ridge on the posterior surface of the principal cusp divides this surface into two parts. When the specimen was collected this tooth was loosely attached and on removal disclosed a small bit of enamel of a permanent tooth beneath. In front of $Dp\overline{3}$ is the exposed cross-section of the anterior premolar and presumably the canine. $P\overline{4}$ is the largest tooth of the series, $P\overline{4}$–$M\overline{3}$ inclusive. In this tooth only a vestige of the paraconid ridge remains and the metaconid does not reach the height of the protoconid. The basin of the talonid is deeply excavated. This tooth and the molars which follow all show a well defined cingulum at the base of the protoconid and below the notch between this cusp and the hypoconid. In $M\overline{3}$ the posterior wall of the hypoconulid is broken away. The ramus is sturdy and of approximately same depth

---

PLATE 1

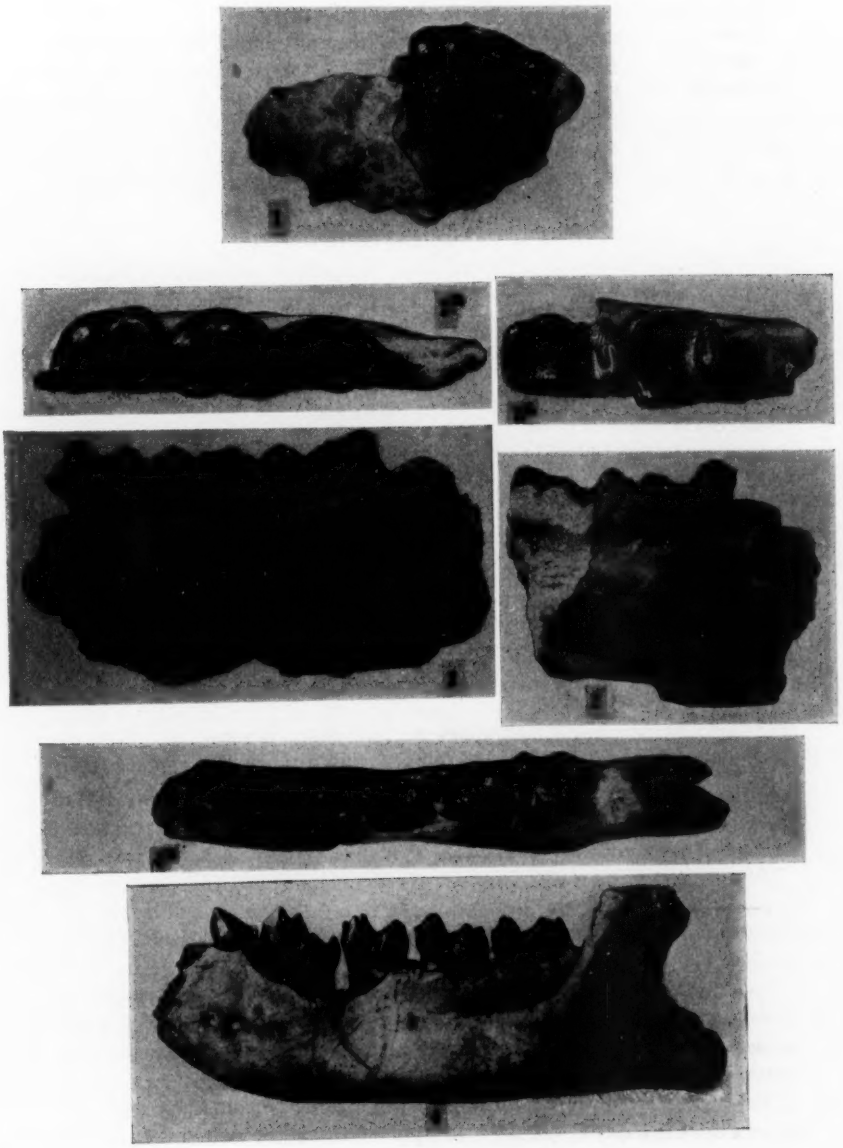
Yumanius woodringi, n. gen. and n. sp.

Figure 1, type specimen, No. 2233, skull fragment with $M\underline{2}$ and $M\underline{3}$, occlusal view. Figures 2, 2*a*, No. 2234, jaw fragment with $M\overline{1}$–$M\overline{3}$, view of inner side and occlusal view. Note: In figure 2*a*, the paraconid of $M\overline{1}$ has been restored. Figure 3, 3*a*, No. 2235, outer and occlusal views. All figures approximately ×6.

Microsyops kratos, n. sp.

Figures 4, 4*a*, type specimen, No. 2232, ramus with cheek teeth, lateral and occlusal views, ×2.

Calif. Inst. Tech. Vert. Pale. Coll. Poway Eocene, San Diego Co., Calif.



throughout its length. Two mental foramina are situated below the anterior premolars.

Microsyops elegans from the Bridger, as represented by No. 12590, A. M. N. H., is a distinctly smaller, more slender form than the type from the Poway. In the former specimen the lower end of the symphyseal contact surface extends farther back than in No. 2232 from the Poway Eocene, and the second premolar is not crowded between adjacent teeth as in the latter. Moreover, there appears to be less discrepancy in length

COMPARATIVE MEASUREMENTS (IN MILLIMETERS)

	Microsyops kratos	*Microsyops elegans*	*Microsyops annectens*	*Craseops sylvestris*
	TYPE SPECIMEN		TYPE SPECIMEN	
	No. 2232 C. I. T.	No. 12590 A. M. N. H.	No. 11791 Y. P. M.	No. 1399 C. I. T.
Length from anterior end $Dp\overline{3}$ to posterior end of $M\overline{3}$	[a]28.7	....	....	....
Length from anterior end $P\overline{2}$ to posterior end of $M\overline{3}$	....	20.4	....	....
Length from anterior end $P\overline{3}$ to posterior end of $M\overline{3}$	....	18	....	....
Length from anterior end $P\overline{4}$ to posterior end of $M\overline{3}$	[a]24.8	15	....	....
$Dp\overline{3}$, length	3.9	....	....	....
$Dp\overline{3}$, width	2.4	....	....	....
$P\overline{4}$, length	6.6	3.6	....	....
$P\overline{4}$, width	4.2	2.6	....	....
$M\overline{1}$, length	5.5	3.5	....	....
$M\overline{1}$, width	4	2.4	....	....
$M\overline{2}$, length	6	....	....	6.3
$M\overline{2}$, width	4.2	3	....	4.6
$M\overline{3}$, length	[a] 6.2	4.5	5.7	7.1
$M\overline{3}$, width	3.9	3	3.5	4.5
Depth of ramus at posterior end of $M\overline{3}$	11.5	9	11.4	15
Depth of ramus at anterior end of $M\overline{2}$	10.9	8.2	....	14.2
Thickness of ramus below $M\overline{2}$	6.1	4.2	....	6.9
Thickness of ramus below $M\overline{3}$	6.2	....	4.5	8

[a] Approximate

between $P\overline{4}$ and $M\overline{1}$ in the Bridger species than in that from the San Diego locality.

No. 12050 A. M. N. H., also from the Bridger Eocene and determined as *Microsyops annectens*, approaches the Poway specimen in size. While the ramus exhibits a depth like that in the Californian type, its thickness is distinctly less.

No. 1399 C. I. T., representing *Craseops sylvestris* from the Sespe possesses a more massive ramus with the upper anterior border and the anterior end of the masseteric area decidedly more pronounced than in *Microsyops*

kratos. The two molar teeth preserved in No. 1399, $M\overline{2}$ and $M\overline{3}$, are slightly broader in comparison to their length in *Craseops* than in *Microsyops* from the Poway.

[1] Stock, C., *Proc. Nat. Acad. Sci.*, **23**, 48–53 (1937).
[2] Wortman, J. L., *Amer. Jour. Sci.*, Ser. 4, **17**, 139–140, fig. 133 (1904).
[3] Matthew, W. D., and Granger, W., *Bull. Amer. Mus. Nat. Hist.*, **34**, 457 (1915).

LARGEST DEGREE OF A SUBSTITUTION IN THE GROUPS OF A GIVEN DEGREE

BY G. A. MILLER

DEPARTMENT OF MATHEMATICS, UNIVERSITY OF ILLINOIS

Communicated May 28, 1938

Let G represent a substitution group of degree n and let s represent a substitution of G which has the property that none of the substitutions of G has a degree which exceeds that of s. It follows directly from the average number of letters in the substitutions of a given group that the degree of s cannot be less than $n/2 + 1$. It has recently been proved[1] that when the degree of s has this smallest possible value, then all the substitutions of G besides the identity are of the same degree and G is an abelian group whose order is a power of 2. Moreover, n must then be of the form $2^m + 2^{m-1} + \ldots + 2$ and there is one and only one such group for an arbitrary positive integral value of m. The order of this group is 2^m and it is conformal with the abelian group of type 1^m. Every substitution besides the identity of an arbitrary one of this infinite system of groups has exactly half of its letters in common with every other substitution besides the identity of this group whenever $m > 2$.

When the degree of s exceeds $n/2 + 1$ it is at least as large as $n/2 + 3/2$, and when it has this value there are only three possible groups, viz., the two groups of degree 3 and the nonabelian group of degree 5 and of order 6 whose transitive constituents are of degrees 2 and 3, respectively. As this fact was also established in the article to which we referred above, the smallest possible relative degree of s which has not been considered is $n/2 + 2$. When the degree of s is $n/2 + 1$ the group of degree 2 is the only possible transitive group, and when it is $n/2 + 3/2$ the two groups of degree 3 are the only possible transitive groups. It is obvious that when the degree of s is $n/2 + 2$ then the five transitive groups of degree 4 are the only possible transitive groups but there are then two intransitive groups in addition to three infinite systems of such groups whose degrees are of the

form $2^m + 2^{m-1} + \ldots + 4$, $m > 2$, in two cases, and of the form 2^{m+1} in the third case. In one of the first two cases the order of G is 2^{m-1} while in the other it is 2^m. In the third case the order of G is also 2^m.

Each of the possible groups of degree 4 has the property that its substitutions of highest degrees are of degree $n/2 + 2$. Hence it may be assumed in what follows that $n > 4$ unless the contrary is stated. If at least one of the transitive constituents of G is of odd degree and the substitution of highest degree in G is of degree $n/2 + 2$, then two of the transitive constituents of G are of degree 3. Each of the remaining transitive consituents of G is then of degree 2 and hence the average number of letters in the substitutions of G is $n/2 + 1$. The value of n cannot exceed 8 because not more than four of the letters of the substitution of largest degree could appear in the group whose transitive constituents are 3, 3, and when $n = 8$ there are obviously two such groups of orders 6 and 18, respectively. Hence there are two and only two groups of degree n in which a substitution of highest degree is of degree $n/2 + 2$ and which involve separately at least one transitive constituent of odd degree. The transitive constituents of these groups are of degrees 2, 3, 3, respectively.

It remains to determine the groups of degree n whose substitutions of largest degrees involve $n/2 + 2$ letters and all of whose transitive constituents are of even degrees. The largest value of such a degree is 4 and not more than one of the transitive constituents of G can be of this degree. If G contains one such constituent and $n > 4$ its remaining constituents are of degree 2 and hence s involves at least $(n - 4)/2 + 1$ letters from this constituent. This is impossible since it involves 4 letters from the transitive constituent of degree 4. It results therefore that when the degree of s is $n/2 + 2$ and each of the transitive constituents of G is of even degree then all of these degrees are equal to 2 whenever $n > 4$. It remains only to consider the cases when each of the transitive constituents of G is of degree 2 and when G is therefore an abelian group.

The fundamental infinite system of such groups can then be constructed by choosing for s a substitution of degree 2^m, $m > 2$, and extending it by a substitution of the same degree which has half its letters in common with s just as in the case when the substitution of largest degree in G is of degree $n/2 + 1$. When $m > 2$ we extend this group of order 4 by a substitution which has half of its letters in common with each of the three substitutions of order 2 in this group of order 4. This process is repeated until each of the substitutions has four and only four letters in common with every other one while the separate pairs have half of their letters in common. The resulting group is of degree $2^m + 2^{m-1} + \ldots + 4$ and of order 2^{m-1}. All of its substitutions, besides the identity, are of degree 2^m. By extending this group by a substitution of degree $2^m - 2$ which has two letters in common with each of its substitutions but involves no additional letter

there results a group of order 2^m and of degree $2^m + 2^{m-1} + \ldots + 4$ whose substitution of largest degree involves $n/2 + 2$ letters.

Half of the substitutions of the latter group are negative and are of the same degree. The smallest two groups which belong to this system are the intransitive group of degree 4 and of order 4, and the group of degree 12 and of order 8 which involves four substitutions of degree 6 but no substitution of a larger degree than 8. To obtain the third infinite system of groups of degree n whose substitution of largest degree is of degree $n/2 + 2$ we adjoin to an arbitrary group of the former of the two infinite systems noted in the preceding paragraph a substitution of degree $2^m + 4$ which has two letters in common with each of its substitutions but involves four additional letters. The smallest group which belongs to this system is of order 4 and of degree 8. *There are therefore two infinite systems of groups of degree* n *in which the substitution of largest degree is of degree* $n/2 + 2$ *whenever* n *is of the form* $2^m + 2^{m-1} + \ldots + 4$. *When* n *is of the form* 2^{m+1} *there is an additional such system of groups.*

To prove that these three infinite systems of groups include all of the groups of degree n in which the substitutions of largest degree are of degree $n/2 + 2$ and each of the systems of intransitivity is of degree 2, it is desirable to consider separately the three cases in which G is composed of the substitutions of highest degree together with the identity, in which the substitutions of highest degree generate a proper subgroup of G, and in which these substitutions generate G but G involves also substitutions which are not of highest degree. In each of these cases G involves at least $n/4$ substitutions of highest degree since the average number of the letters in its substitutions is $n/2$ and hence it must involve $n/4$ substitutions of highest degree to account for the fact that the identity is of zero degree, since each substitution of highest degree involves two more letters than the average.

When all the substitutions of G besides the identity are of degree $n/2 + 2$ then this degree is 2^m since every two substitutions of order 2 contained in G have half of their letters in common. It therefore results that $n = 2^m + 2^{m-1} + \ldots + 4$ and the order of G is 2^{m-1}. Hence G is one of the groups of the first of the three infinite systems noted above whenever it is composed of its substitutions of highest degree together with the identity. It is obvious that a substitution s which has two letters in common with each of the substitutions of order 2 in such a G is negative and of degree $n/2$. The products of s into all the substitutions of G give all of the substitutions which have this property with respect to a given G and hence there results a group which is completely determined by the given G and of twice its order. This group belongs to the second of the infinite system noted above and all of the groups which can be formed in this way constitute this system.

It remains to consider the case when the substitutions of highest degree

in G generate G but generate also substitutions of lower degree. In this case the substitutions of highest degree are negative since this degree is a power of 2 increased by 2. In fact, if the degree of these substitutions is a power of 2 increased by $2k$ and we construct G as noted above the substitution of highest degree in the resulting group is of the form $n/2 + k + 1$. In this construction we extend successively the group formed by the substitution built on the part of a substitution of largest degree whose degree is a power of 2. It therefore results that the three infinite systems of groups noted above include all the groups of degree n which involve only systems of intransitivity of degree 2 and whose substitutions of largest degree involve exactly $n/2 + 2$ letters. The orders of the groups of the last system are one-half of their degrees.

When the largest degree of a substitution in a group of degree n exceeds $n/2 + 2$ it is at least as large as $n/2 + 5/2$ and when it has this value n is odd and the number of possible groups is infinite since if there is a transitive constituent of degree 3 there is an infinite number of groups on the remaining $n - 3$ letters whose substitutions of largest degree are $(n - 3)/2 + 1$. Hence there is an infinite number of groups on n letters whose substitutions of largest degree are of degree $(n - 3)/2 + 4$ or $n/2 + 5/2$. Such groups can be constructed by forming the direct products or by establishing an isomorphism between the symmetric group of degree 3 and a group whose order is a power of 2 and whose substitutions of largest degree are of degree $(n - 3)/2 + 1$. They can also be constructed by forming the direct products of the alternating group of degree 3 and the latter groups as well as by the direct products of the three groups of degree n whose substitution of largest degree involves $n/2 + 3/2$ letters.

It has been noted that the smallest relative number of letters in a group of degree n appears only when n is of the special form $2^m + 2^{m-1} + \ldots + 2$, and that when n is of the form 2^{m+1} then there are groups whose substitutions of largest degree do not involve more than $n/2 + 2$ letters. From the latter of these theorems it results directly that for an arbitrary value of n there is a substitution group of degree n which does not involve more than $3n/4 + 2$ letters since there is a number which is a power of 2 and exceeds $n/2$. This degree is usually much smaller as follows from repeated applications of the given results.

[1] *Proc. Nat. Acad. Sci.*, **24**, 202–204 (1938).

REMARKS ON RIEMANN'S DOCTORAL DISSERTATION

BY JESSE DOUGLAS

BROOKLYN, N. Y.

Communicated June 10, 1938

1. The author has based the solution of Plateau's problem on the minimum principle

$$D(H) = \int\int \frac{1}{2}(E + G)du\,dv$$

$$= \frac{1}{2}\int\int \sum_{i=1}^{n}\left[\left(\frac{\partial H_i}{\partial u}\right)^2 + \left(\frac{\partial H_i}{\partial v}\right)^2\right] du\,dv = \text{min.}, \qquad (1)$$

among all harmonic vectors $H(u, v)$ which represent a surface bounded by a given contour Γ in n-dimensional euclidean space.[1] The (u, v) domain may be supposed to be the unit circle C.

Explicitly, $D(H)$ may be expressed in terms of the boundary values $g(\theta)$ of H on the unit circumference c by the formula

$$A(g) = \frac{1}{4\pi}\int_c\int_c \frac{\sum_{i=1}^{n}\left[g_i(\theta) - g_i(\varphi)\right]^2}{4\sin^2\dfrac{\theta - \varphi}{2}}\,d\theta d\varphi. \qquad (2)$$

Since, for given boundary values, a harmonic function gives the least value to Dirichlet's integral, the principle (1) is equivalent to

$$D(\mathfrak{x}) = \frac{1}{2}\int\int (\mathfrak{x}_u^2 + \mathfrak{x}_v^2)du\,dv =$$

$$\frac{1}{2}\int\int \sum_{i=1}^{n}\left[\left(\frac{\partial x_i}{\partial u}\right)^2 + \left(\frac{\partial x_i}{\partial v}\right)^2\right] du\,dv = \text{min.}, \qquad (3)$$

where the vector $\mathfrak{x}(u, v)$ may represent any piece-wise continuously differentiable surface bounded by Γ.

If $n = 2$, so that Γ is a plane curve enclosing a region R, then, as was observed by the author, the Plateau problem becomes the one of mapping R on C conformally. Denote by $x(u, v)$, $y(u, v)$ the components of $\mathfrak{x}$; then

$$\mathfrak{A} = \int\int_C (x_u y_v - x_v y_u)du\,dv = \frac{1}{2}\int_\Gamma (x\,dy - y\,dx) \qquad (4)$$

is a constant, equal to the area of R, for all vectors $x(u, v)$, $y(u, v)$ in the unit circle which map the circumference c topologically on Γ.[2] Hence the principle (3) is equivalent to

$$D(\mathfrak{x}) - \mathfrak{A} = \min., \tag{5}$$

or

$$E(x, y) = \int\int_C [(x_u - y_v)^2 + (x_v + y_u)^2]\, du\, dv = \min. \tag{6}$$

Indeed, for a conformal map the Cauchy-Riemann equations

$$x_u - y_v = 0, \qquad x_v + y_u = 0, \tag{7}$$

are satisfied, and $E(x, y) = 0$; while for a non-conformal map, $E(x, y) > 0$.

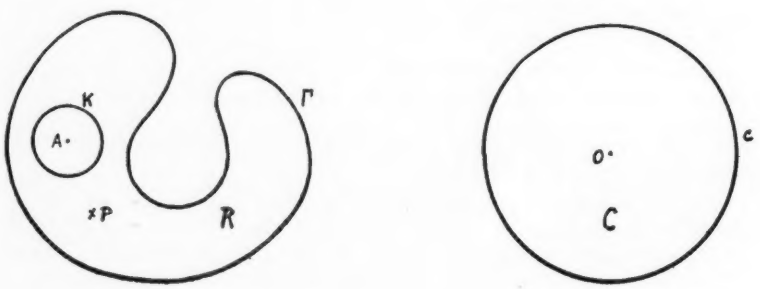
The resemblance which the minimum principle (6) bears to the one considered by Riemann in his dissertation:[3]

$$\Omega(\omega) = \int\int_R [(\omega_x - \beta_y)^2 + (\omega_y + \beta_x)^2]\, dx\, dy = \min., \tag{8}$$

is only superficial. But recently the statement has been made, in reference to (6), that: "This is exactly the famous variational problem which Riemann considered in his doctor's thesis."[4]

In view of the classic character of Riemann's dissertation, and its influence on the entire subsequent development of the theory of conformal mapping, it therefore seems appropriate to point out a number of sharp and essential differences between the principles (6) and (8). To do this is the purpose of the present note.

2. Riemann was seeking a minimum principle to use as a basis for establishing the existence of Green's function $G(P, A)$ of the region R, or the equivalent conformal map of R on the circular region C.



The Green's function is uniquely defined by the properties: (1) harmonic in R; (2) vanishing on Γ; (3) regular in the interior of R, except for a logarithmic singularity at the point A:

$$G(P, A) = \log \rho + h(P, A), \tag{9}$$

where ρ = distance AP, and h is a harmonic function of the point P regular throughout R including the point A. If G_1 denote the conjugate harmonic function to G, i.e.,

$$G_1(P) = -\int_{P_0}^{P} \frac{\partial G}{\partial n}\, ds, \tag{10}$$

then the conformal transformation from R to C is given by the function e^{G+iG_1}.

If Γ is a general type of boundary curve, then the behavior of $\partial G/\partial n$, therefore of G_1, as we approach the boundary is uncertain. Hence the conformal map furnished by Riemann's method subsists only between the *interiors* of the regions involved, and the problem of what type of correspondence is established between the *boundaries* is left open. This problem was solved many years after the work of Riemann by Osgood and by Carathéodory,[5] who proved that the conformal map of the interiors induces by continuity a one–one continuous correspondence between the boundaries.

3. The first suggestion for determining G by means of a minimum condition might be to use the Dirichlet principle as it stands:

$$D(\omega) = \int\int_R (\omega_x^2 + \omega_y^2)\, dx\, dy = \text{min.}, \tag{11}$$

where we admit to comparison all functions $\omega(x, y)$ of like nature to $G(P, A)$: vanishing on the boundary Γ, and logarithmically singular at A. But since, as is easily verified,

$$D(\log \rho) = +\infty \tag{12}$$

over any neighborhood of A, we have the fundamental difficulty that

$$D(\omega) \equiv +\infty \tag{13}$$

for all functions ω logarithmically singular at A. Hence the original problem (11) *has no sense*.

We need a functional that for at least one value of its argument takes a finite value. Riemann secures this by means of an ingenious device, in the use of which (or similar devices) he has been followed by many subsequent contributors to the theory.[6]

He introduces, instead of $D(\omega)$ = min., the problem (8) $\Omega(\omega)$ = min., where β is a *fixed* function so designed that $\Omega(\omega)$ is finite for at least a particular form of ω. *Regardless of the parameter function* β, this problem has the same variational equation as $D(\omega)$ = min., namely,

$$\frac{\partial}{\partial x}(\omega_x - \beta_y) + \frac{\partial}{\partial y}(\omega_y + \beta_x) = \omega_{xx} + \omega_{yy} = 0, \tag{14}$$

or Laplace's equation. The function β simply cancels out in the formation of the variational condition.

Riemann's idea was to arrange β so that $\Omega(\omega)$ will be finite for at least one particular form of ω. This he accomplished by choosing β to coincide in a small circle[7] K about A as center with the conjugate harmonic function to the one, $\log \rho$, that characterizes the singularity at A, namely,

$$\beta(x, y) = \tan^{-1} \frac{y}{x} \tag{15}$$

(we have taken A to be the origin). In $R - K$, β may be any smooth function which (1) like $\tan^{-1} y/x$, has a period of 2π with respect to a cut L in R that leads from A to the boundary Γ, and (2) which attaches smoothly to $\tan^{-1} y/x$ at the circumference of K. The simplest choice is to define β by the formula (15) throughout the region R as provided with the cut L. That β is multiform is no serious inconvenience, since only its partial derivatives are used, which are uniform:

$$\beta_x = \frac{-y}{x^2 + y^2}, \qquad \beta_y = \frac{x}{x^2 + y^2}. \tag{16}$$

Riemann then selects as particular form of ω a function α defined and smooth throughout R except at the point A, equal to $\log \rho$ in the circle K, and reducing to zero on Γ.[8] Then, precisely because of the prearranged conjugacy between β and $\log \rho$ in the circle K, we have in that circle.

$$\alpha_x - \beta_y = 0, \qquad \alpha_y + \beta_x = 0; \tag{17}$$

therefore

$$\Omega(\alpha) = 0 \textit{ over } K. \tag{18}$$

Since the partial derivatives of α and β are bounded and continuous[9] in the rest of the region, $R - K$, it follows that

$$\Omega(\alpha) = \textit{finite quantity}. \tag{19}$$

Thus Riemann concludes that the problem (8) *has sense*. The minimizing function ω^*, if existent,[10] will then obey Laplace's equation, and this, together with its vanishing on Γ and logarithmic singularity at A, characterizes ω^* as Green's function $G(P, A)$.

4. The preceding discussion may be summarized as follows.

In the problem $\Omega(\omega) = \text{min.}$ considered by Riemann, β *is entirely fixed*, and the *only* function in competition is ω, which varies subject to the *fixed boundary values zero* and logarithmic singularity at A.

But in the problem $E(x, y) = \text{min.}$,

(1) $x(u, v)$, $y(u, v)$ are *both variable* in competition with other function-pairs;

(2) the boundary values of x, y are *not fixed*, but vary simultaneously subject to the restriction of always defining a topological correspondence between Γ and c.

More important is the following distinction.

(3) In Riemann's problem, the argument function $\omega(x, y)$ is defined in the *generally complicated region* R, and the sole and entire purpose of the problem is to obtain the Green's function of R by identifying it with the minimizing function ω^*.

But in the problem $E(x, y) = \text{min.}$, the argument functions are defined in the *circular region* C, where we have no need to find Green's function, since that is known by elementary geometry:

$$G(P, A) = \log \frac{AP}{A_0P} - \log \frac{AI}{A_0I}, \tag{20}$$

A_0 denoting the inverse point of A, and I the point $(1, 0)$.

Since $E(x, y)$ differs only by a constant from the sum of Dirichlet integrals $D(x) + D(y)$, the minimizing functions $x(u, v)$, $y(u, v)$ must be harmonic, and are therefore determined by Poisson's integral as soon as their *boundary values* $x(\theta)$, $y(\theta)$ are known. Thus, the real point in connection with $E(x, y) = \text{min.}$ is to find what topological correspondence shall be established by $x(\theta)$, $y(\theta)$ between Γ and c.

The author has expressed this in an explicit way by the principle (2) $A(g) = \text{min.}$, where g denotes the vector with the components $x(\theta)$, $y(\theta)$. The *direct* treatment of this minimum problem is safe from the Weierstrass criticism,[11] since the argument range $[g]$ is *compact*,[12] whereas the argument range $[\omega]$ of Riemann's problem is *not*.[13] Accordingly, the existence of the minimizing vector $x^*(\theta)$, $y^*(\theta)$ is easily established, and the conformal transformation from C to R is then given immediately by the Poisson integrals for $x^*(\theta)$ and $y^*(\theta)$, or by the equivalent Cauchy formula

$$W = \frac{1}{2\pi i} \int_c [x^*(\theta) + iy^*(\theta)] \frac{dz}{z - w} \qquad (z = e^{i\theta}). \tag{21}$$

(4) The minimum problem of Riemann gives, when solved, only a correspondence between the *interiors* of R and C. Supplementary considerations of quite different character were necessary to extend this correspondence by continuity to the *boundaries*. In fact, the topological nature of the boundary correspondence was only established by Osgood and by Carathéodory a number of years after the rigorous solution of the Riemann-Dirichlet minimum problem by Hilbert.[14]

But in the problem $E(x, y) = \text{min.}$, the very nature of the argument functions, as prescribed, must *automatically* give a topological correspon-

dence between the boundaries simultaneously with the conformal map of the interiors.

5. In conclusion, no basis remains for identifying the problem (6) $E(x, y) = \text{min.}$ with the one considered by Riemann in his famous dissertation.

[1] J. Douglas, *Trans. Amer. Math. Soc.*, **33**, 263–321 (1931); *Bull. Amer. Math. Soc.*, **39**, 227–251 (1933).

[2] This is regardless of whether the locus of the point (x, y) covers the region R simply or multiply, or extends outside that region. To assure the existence of the curvilinear integral in (4), we may suppose Γ to be rectifiable, but the fact of the constancy of $\mathfrak{A}$ applies when Γ is any Jordan curve.

[3] B. Riemann, *Grundlagen für eine allgemeine Theorie der Functionen einer veränderlichen complexen Grösse*, Göttingen, 1851. *Gesammelte Werke*, 1892. See especially §§16, 18, 21.

[4] R. Courant, *Ann. Math.*, **38**, 696 (1937), where the transformation from (3) to (6) is given. See also Courant-Hilbert, *Methoden der Mathematischen Physik*, **2**, 536–537 (1937).

[5] W. F. Osgood and E. H. Taylor, *Trans. Amer. Math. Soc.*, **14**, 277–298 (1913); C. Carathéodory, *Math. Annalen*, **73**, 305–320 (1913).

[6] Notably Weyl; see *Die Idee der Riemannschen Fläche*, 1913, p. 92.

[7] One whose radius is less than the distance from A to Γ.

[8] In Riemann's presentation, $\alpha + i\beta$ is chosen equal to $\log (x + iy)$ in the circle K (called Θ by Riemann), which is equivalent to the separate conditions $\alpha = \log \rho$, $\beta = \tan^{-1} y/x$. Riemann's stipulation (loc cit., p. 41) that $\alpha + i\beta$ be pure imaginary on the boundary of R is, of course, equivalent to: $\alpha = 0$ on Γ. The region R is called T by Riemann.

[9] We may even take α to be zero in a region adjacent to the boundary Γ, as well as upon it.

[10] We have in mind the remark of Weierstrass, which emphasized the necessity of proving rigorously the *attainment* of the minimum. This was not accomplished until about 1900 by Hilbert, "Über das Dirichletsche Prinzip," *Math. Annalen*, **59**, 161–186.

[11] See footnote 10.

[12] Every sequence of elements g contains a convergent sub-sequence.

[13] For a fuller discussion of this point, see the second reference in footnote 1.

[14] See footnotes 5 and 10.

INFORMATION TO CONTRIBUTORS

THE PROCEEDINGS is the official organ of the NATIONAL ACADEMY OF SCIENCES and of the NATIONAL RESEARCH COUNCIL for the publication of brief accounts of important current researches of members of the ACADEMY and of the COUNCIL and of other American investigators. The PROCEEDINGS will aim especially to secure prompt publication of original announcements of discoveries and wide circulation of the results of American research among investigators in other countries and in all branches of science.

ARTICLES should be brief. The viewpoint should be comprehensive in giving the relation of the paper to previous publications of the author or of others and in exhibiting, where practicable, the significance of the work for other branches of science. Elaborate technical details of the work and long tables of data should be avoided, but authors should be precise in making clear the new results and should give some record of the methods and data upon which they are based.

MANUSCRIPTS should be prepared with a current number of the PROCEEDINGS as a model in matters of form, and should be typewritten in duplicate with double spacing, the author retaining one copy. Illustrations should be confined to text-figures of simple character, though more elaborate illustrations may be allowed in special instances to authors willing to pay for their preparation and insertion. Particular attention should be given to arranging tabular matter in a simple and concise manner.

REFERENCES to literature, numbered consecutively, will be placed at the end of the article and short footnotes should be avoided. It is suggested that references to periodicals be furnished in some detail and in general in accordance with the standard adopted for the Subject Catalogue of the International Catalogue of Scientific Literature, viz., name of author, with initials following (ordinarily omitting title of paper), abbreviated name of Journal, with place of publication, series (if any), volume, inclusive pages, year. For example: Montgomery, T. H., *J. Morph., Boston*, **22**, 731–815 (1911); or, Wheeler, W. M., *Konigsburg, Schr. physik., Ges.*, **55**, 1–142 (1914).

PAPERS by members of the ACADEMY may be sent to Edwin Bidwell Wilson, Managing Editor, Harvard School of Public Health, Boston 17, Mass. Papers by non-members of the ACADEMY or COUNCIL should be submitted through some member.

PROOF will not ordinarily be sent; if an author asks for proof, it will be sent with the understanding that charges for his corrections shall be billed to him. Authors are therefore requested to make final revisions on the typewritten manuscripts. The editors cannot undertake to do more than correct obvious minor errors.

REPRINTS should be ordered at the time of submission of manuscript. They will be furnished to authors at cost, approximately as follows:

SCHEDULE OF RATES FOR REPRINTS, CARRIAGE CHARGES EXTRA

No. copies	50	100	150	200	250
4 pp.	$2.10	$2.40	$2.70	$3.00	$3.30
8 pp.	4.20	4.80	5.40	6.00	6.60
Covers	1.60	2.05	2.50	2.95	3.40

CONTENTS

Page

GENETICS.—THE DISTRIBUTION OF GENE FREQUENCIES UNDER IRREVERSIBLE MUTATION . . . . . *By Sewall Wright* 253

PHYSIOLOGY.—AUXIN IN ISOLATED ROOTS GROWING IN VITRO . . . . . *By J. van Overbeek and James Bonner* 260

PHYSICS.—THE MECHANISM OF HEARING AS REVEALED THROUGH EXPERIMENT ON THE MASKING EFFECT OF THERMAL NOISE . . *By Harvey Fletcher* 265

PHYSICS.—THE DIMENSIONLESS CONSTANTS OF PHYSICS . *By Arthur E. Haas* 274

PSYCHOLOGY.—ON THE RELATIVE CONTRIBUTIONS OF NATURE AND NURTURE TO AVERAGE GROUP DIFFERENCES IN INTELLIGENCE . *By Barbara S. Burks* 276

ASTRONOMY.—A METAGALACTIC DENSITY GRADIENT . . *By Harlow Shapley* 282

PALEONTOLOGY.—A TARSIID PRIMATE AND A MIXODECTID FROM THE POWAY EOCENE, CALIFORNIA . . . . . *By Chester Stock* 288

MATHEMATICS.—LARGEST DEGREE OF A SUBSTITUTION IN THE GROUPS OF A GIVEN DEGREE . . . . . *By G. A. Miller* 293

MATHEMATICS.—REMARKS ON RIEMANN'S DOCTORAL DISSERTATION . . . *By Jesse Douglas* 297